The taxonomic history of the enigmatic Papuan snake genus *Toxicocalamus* (Elapidae: Hydrophiinae), with the description of a new species from the Managalas Plateau of Oro Province, Papua New Guinea, and a revised dichotomous key

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Abstract: We trace the taxonomic history of *Toxicocalamus*, a poorly known genus of primarily vermivorous snakes found only in New Guinea and associated island archipelagos. With only a relatively limited number of specimens to examine, and the distribution of those specimens across many natural history collections, it has been a difficult task to assemble a complete taxonomic assessment of this group. As a consequence, research on these snakes has undergone a series of fits and starts, and we here present the first comprehensive chronology of the genus, beginning with its original description by George Albert Boulenger in 1896. We also describe a new species from the northern versant of the Owen Stanley Range, Oro Province, Papua New Guinea, and we present a series of comparisons that include heretofore underused characteristics, including those of unusual scale patterns, skull details, and tail tip morphology. Defined by the smallest holotype in the genus, the new species is easily differentiated from all other *Toxicocalamus* by a combination of the following eidonomic characters: fused prefrontal-internasal scute; single preocular, separate, not fused with prefrontal; minute circular, counter-sunk naris in the centre of a large, undivided, nasal scute; paired postoculars; single anterior temporal and paired posterior temporals; six supralabials, with 3rd and 4th supralabial contacting the orbit; dorsal scales in 15-15-15 rows; 235 ventral scales, 35 paired subcaudal scales; paired cloacal scales preceded by paired precloacal scales; and a short, laterally slightly compressed, '*Ultrocalamus*-type' tail, terminating in a short conical scale. Differences from congeners in skull morphology include a reduced anterior extent of the parasphenoid, termination of the palatine tooth row at the anterior level of the parasphenoid, extent and shape of the premaxilla, shape and size of the prootics, extent and shape of the exoccipitals and occipital condyles, and features of the atlas-axis complex. This is the fifteenth species in the genus *Toxicocalamus*.

Keywords: taxonomy, fossorial snakes, pholidosis, Melanesia, adaptive radiation

Introduction

The ophidiofauna of New Guinea, including Papua New Guinea (PNG) and the provinces of Papua and West Papua of Indonesian West New Guinea (WNG), is very diverse and includes a significant proportion of terrestrial elapids (e.g., O'Shea, 1996). Thirteen terrestrial elapid genera, represented by a total of 31 species, inhabit the Melanesian region, from New Guinea to the Solomon Islands, exclusive of continental Australia. Six of these genera are endemic to the region, of which three (*Aspidomorphus*, *Micropechis*, and *Toxicocalamus*) are endemic to New Guinea, including the Bismarck, d'Entrecasteaux, and Louisiade archipelagos located to the east and southeast. The remaining three (*Loveridgelaps*, *Parapistocalamus,* and *Salomonelaps*) occur only in the Solomon Island archipelago (including the islands of Bougainville and Buka in PNG). With 14 currently recognised species (Uetz et al., 2018), *Toxicocalamus* is the most diverse terrestrial Melanesian elapid genus. Its distribution extends from the Fakfak Mountains of West Papua Province, WNG, through the north and centre of New Guinea, including the offshore Seleo Island (Sandaun Province, PNG), Walis and Tarawai Islands (East Sepik Province, PNG), and Karkar Island (Madang Province, PNG), to the southeastern tip of the Papuan Peninsula, and the islands of Milne Bay Province (PNG), including the d'Entrecasteaux Archipelago (Goodenough, Fergusson, and Normanby Islands), Woodlark Island, and the Louisiade Archipelago (Misima, Sudest, and Rossel Islands) (Figure 1).

Toxicocalamus appears to be absent from the Vogelkop and Raja Ampat Archipelagos (West Papua Province, WNG), the Schouten Islands of Cenderwasih (formerly Geelvink) Bay (Papua Province, WNG), the seasonally flooded savannas of the southern Trans-Fly Region (southern Western Province, PNG, and southeastern Papua Province, WNG), the Torres Strait Islands (Daru and Bobo Islands, Western Province, PNG, and Saibai, Boigu, and Dauan Islands, Queensland, Australia), the Admiralty Archipelago (Manus Province, PNG), the Bismarck Archipelago (Umboi Island in Morobe Province, West and East New Britain Provinces[1], and New Ireland Province, all PNG), Bougainville, and the Solomon Islands. It is likely that the actual number of species in the genus is considerably greater than currently listed, with new taxa awaiting discovery and description both in the field and in museum collections.

Snakes in the genus *Toxicocalamus* are generally not commonly encountered, although large numbers of specimens have been collected at occasional highland localities (e.g., the fertile valleys surrounding Kundiawa, Simbu Province, PNG). Very little is known about their natural history (e.g., Shine and Keogh, 1996; Allison et al., 1998). As members of the family Elapidae, it is particularly relevant for humans that we briefly comment on the toxicity of these fossorial species. A toxin protein analysis has been completed for only one species (*T. longissimus*; Calvete et al., 2012), and its toxin cocktail was found to be quite potent. Furthermore, the venom glands in at least *T. buergersi* are very large, extending along the entire anterior third of the body (Calvete et al., 2012), and thus, there appears to be potency in both quality of venom composition and quantity of venom delivery. Anecdotal evidence has shown that several species have an affinity for large earthworms as prey (e.g., Calvete et al., 2012;

[1] There is a specimen in existence (IRSNB 18737) that was purportedly collected at Uasilau, West New Britain, in the Bismarck Archipelago, with the locality indicated in Figure 1. The validity of this record has yet to be confirmed (MOS & HK, in prep.).

O'Shea et al., 2015; Kraus, 2017) but, given that the process of earthworm consumption does not appear to involve envenomation, the function of such a toxic venom may be defensive. Those encountering these species should therefore exercise great caution.

We have been working on the taxonomy and natural history of *Toxicocalamus* over the last several years (e.g., O'Shea et al., 2015, 2018; O'Shea and Kaiser, 2018) and we have made some significant inroads into an understanding of morphological variation. As a consequence of having examined 497 of the 513 *Toxicocalamus* specimens currently housed in natural history collections, we are now better able to draw some interspecific boundaries for specimens of uncertain affinities. This paper is a result of our historical approach and our morphological methodology, as we continue to fine-tune the taxonomy of the genus.

A Chronology of the Genus *Toxicocalamus*

The first decade (1896–1905): four genera and the first problems

The genus *Toxicocalamus* was erected by the Anglo-Belgian zoologist George Albert Boulenger (1858–1937) for his new elapid species *Toxicocalamus longissimus* Boulenger, 1896, a description based on two female syntypes (BMNH 1946.1.18.92–93[2], formerly BMNH 96.7.8.17–18) that had been collected by the British naturalist

[2] At the outbreak of World War II, the British Museum of Natural History, now simply The Natural History Museum, moved as many specimens as possible to places of safety, including Tring Museum and stately homes around the country, to avoid their destruction if the museum suffered a direct bombing hit, which it did on several occasions. Glass jars containing specimens in 70% ethanol were deemed to represent a significant fire risk and might have been less welcome stored in inhabited buildings, so caves or mines were also used. It was reported to the Trustees of the BMNH that "... type specimens in spirit were removed from all Sections of the Department in the autumn of 1941 and deposited packed in wooden boxes and sawdust in a disused hearth-stone mine at Godstone, Surrey." The process of moving the type material took five weeks, while non-type material was moved to basement areas of the museum (Long, 1981). When the type specimens were returned to the collection they were re-accessioned back into the collection, with new accession numbers, in the case of the snakes with a 1946 prefix. The original accession number tags were, of course, left *in situ*.

and ornithologist Albert Stewart Meek (1871–1943) on Woodlark Island (Boulenger, 1896; Figure 1, Locality 7) in what is now Milne Bay Province, PNG. The latter of these two specimens (BMNH 1946.1.18.93), was designated as the "holotype" (= lectotype) by McDowell (1969) because "with the skull extracted and cleaned, [it] must have served as the type of Boulenger's generic diagnosis". Two years later he described *Apisthocalamus loriae* Boulenger, 1897, from a male holotype (MSNG 29141), collected by the Italian anthropologist Lamberto Loria (1855–1913) at Haveri (Figure 1, Locality 8) in what is now Central Province, PNG (Boulenger, 1897). Two years later, the Swedish zoologist Einar Lönnberg (1865–1942) coined the generic name *Pseudapistocalamus* for a new species he named *P. nymani* Lönnberg, 1900, for his late countryman, the botanist Erik Nyman (1820–1893), who had collected the type series at Sattelberg on the Huon Peninsula (Figure 1, Locality 8c) of what is now Morobe Province, PNG, during a botanical expedition (Lönnberg, 1900). There is some confusion over the original type series, which was reported to comprise three specimens, although there are four specimens, three females, one male, in three museum collections labelled as cotypes (BMNH 1946.1.17.57, formerly BMNH 1900.9.21.6; MCZ R-76627–28; UPSZ 2387).

In 1903 and 1904 Boulenger named two additional species of secretive elapids, both collected by the British entomologist and naturalist Antwerp Edgar Pratt (1852–1924) along the St. Joseph's (now Angabanga) River[3] in the Owen Stanley Range (Boulenger, 1903, 1904; Figure 1, Locality 8d), Central Province, PNG. These two species, *T. stanleyanus* Boulenger, 1903 and *Apisthocalamus pratti* Boulenger, 1904, were

[3] The position of Dinawa, on the St Joseph's River, is indicated on a map in Pratt (1906) and further pinpointed by coordinates in Horn et al. (2007).

described from their respective holotypes, a female (BMNH 1946.1.7.55, formerly BMNH 1903.3.10.18) and male (BMNH 1946.1.14.53 formerly BMNH 1904.3.17.12).

In 1905 the genus *Vanapina* was erected for the species *Vanapina lineata* De Vis, 1905, described from a single specimen reportedly collected in the Vanapa Valley, 40 km N Port Moresby, PNG, by Sir William MacGregor (1846–1919), Administrator (1888–1895), later Lieutenant-Governor (1895–1898), of British New Guinea (De Vis, 1905). The holotype was believed to have been accessioned into the Queensland Museum, but it appears to be no longer extant. *Vanapina lineata* was later synonymised with *T. longissimus* by Ingram (1989) based on the published description of the holotype, an unlikely scenario given that the latter is known only from Woodlark Island[4]. In the absence of De Vis's specimen and any other material, it is impossible to determine whether *V. lineata* is a valid species.

The second decade (1908–1914) and the first dichotomous key

In 1908, Boulenger made his fifth contribution to this complex. *Apisthocalamus loennbergii* Boulenger, 1908 was described using four female cotypes (BMNH 1946.1.18.24–26, formerly BMNH 1908.6.30.7–10; MCZ R-76634), collected by A.E. Pratt at Fakfak on the Onin Peninsula (Boulenger, 1908; Figure 1, Locality 8b), now West Papua Province, WNG. In this paper Boulenger distinguished between the genera *Toxicocalamus*, *Apisthocalamus*, and *Pseudapistocalamus* (misspelled as *Pseudapisthocalamus*), using characteristics of their body and head scalation, which he used to formulate a dichotomous key to the six known species: *Apisthocalamus loriae,*

[4] *Toxicocalamus longissimus* is known from twelve specimens, all except one from Woodlark Island. The remaining specimen (BMNH 1904.11.1.60) was reportedly collected on Fergusson Island in the d'Entrecasteaux Archipelago, by A. S. Meek, who also collected the Woodlark type series. It seems probable that the locality was incorrectly reported (O'Shea and Kaiser, 2018).

A. pratti, A. loennbergii, *Pseudapistocalamus nymani, Toxicocalamus stanleyanus*, and *T. longissimus*. He defined the genera as *Apisthocalamus* – preocular present, the nostril between two nasal scales, and 15 dorsal scale rows at midbody; *Pseudapistocalamus* – preocular present, the nostril in a single nasal scale, and 15 dorsal scale rows at midbody; and *Toxicocalamus* – preocular absent, the nostril between two nasal scales, and 15 or 17 dorsal scale rows at midbody. However, Boulenger (1908) noted that it was "… still doubtful whether *Apisthocalamus* and *Pseudapisthocalamus* [sic] can be regarded as valid genera, so closely are they related to the previously described *Toxicocalamus*," but he did not synonymise either genus.

A new genus, *Ultrocalamus*, was described in 1913 by the German herpetologist Richard Sternfeld (1884–1943), who tragically died in the Holocaust (Adler, 2007:137). He defined the type species as *Ultrocalamus preussi* Sternfeld, 1913, which he named after the Polish-born German naturalist Paul Preuss (1861–1926), who collected the holotype (ZMB 23948) on Seleo Island (Sternfeld, 1913; Figure 1, Locality 13), opposite Berlinhafen, now Aitape, Sandaun Province, PNG. In the same paper, Sternfeld (1913) described a second species, *U. buergersi* (using the nomenclaturally inadmissible German spelling *bürgersi*), named for Theodor Joseph Bürgers (1881–1954), the German physician and naturalist on the Kaiserin-Augusta-Fluß-Expedition to the Sepik River in 1912–1913, who had collected the holotype (ZMB 25232; Figure 1, Locality 2). While the specific locality is unknown, the specimen was certainly collected on that expedition, during which approximately 400 km of the Sepik River were explored. The following year, Boulenger (1914) described his sixth and final species of the complex, the largest species at that point, *Toxicocalamus grandis* Boulenger, 1914, known only from its holotype (BMNH 1946.1.18.34, formerly BMNH 1913.11.1.11) and collected during the second

Wollaston Expedition at Launch Camp[5] on the Setekwa River (Figure 1, Locality 4), on the southern coast of what is now Papua Province, WNG.

The period 1928–45: species, subspecies, and synonyms

The Australian herpetologist James Roy Kinghorn (1891–1983) described *Apisthocalamus lamingtoni* Kinghorn, 1928, a new species with a novel feature: the presence of a single cloacal scale[6]. This species was described (Kinghorn, 1928) from an adult and two juveniles (AM R9351–52, R9851) collected on the slopes of Mt. Lamington (Figure 1, Locality 8a), now Oro Province, PNG, by the Resident Magistrate and former Plantation Inspector Charles Terence McNamara (1852–ca. 1920). In the following year the German ornithologist Ernst Schüz (1901–1990) described *Ultrocalamus latiquamatus* Schüz, 1929 from the Garup River in the Torricelli Mountains (Figure 1, Locality 2a), now Sandaun Province, PNG (Schüz, 1929), based on a single specimen (MTKD 2360) collected by the Swiss anthropologist and

[5] The precise locality of "Launch Camp" is difficult to define. Wollaston (1914) mentioned this camp in the text but it does not appear on the accompanying map, which instead includes two campsites (with latitude and longitude coordinates) on the lower reaches of the Setekwa (or Setakwa) River: an unnamed camp on the confluence of the Setekwa and Utakwa Rivers (4°47'26" S, 137°19'1" E) and "Base Camp" on the confluence of the Setekwa and Monunowa Rivers (4°45'6" S, 137°20'7" E). There is also a location indicated only as "Anchorage" lower down the Setekwa. Any of these could be Launch Camp.

[6] The terminology of these scales warrants a brief comment. Anatomically speaking, the scale covering the cloaca is a cloacal scale and not an anal scale, a commonly occurring misnomer in the snake taxonomy literature. Another misnomer is that the cloacal scale is divided. In a developmental context, scales of squamates are formed from epidermal tissues during embryogenesis (e.g., Swadźba et al., 2009), and each ventral scale is formed independently from an epidermal scale primordium. Thus, the condition of the cloacal scale is paired or single, just as occurs with subcaudal scales. *Toxicocalamus pumehanae* therefore possesses paired cloacal scales. In addition, the species has paired precloacal scales, which would originate from a set of dual scale primordia in the epidermis, distinct from those forming the cloacal scales.

ethnologist Otto Schlaginhaufen (1879–1973). This specimen is no longer extant, having been lost in the Allied bombing of Dresden from 13–15 February 1945.

In 1945 Charles Mitchell Bogert (1908–1992) and Bessie Louise Hecht (née Matalas, b. 1922) synonymised *Ultrocalamus buergersi* and *U. latisquamatus* with *U. preussi* (Bogert and Matalas, 1945), and described a new subspecies, *U. preussi angusticinctus* Bogert & Matalas, 1945 from Palmer Junction on the Upper Fly River (Figure 1, Locality 14), now Western Province, PNG. This taxon was based on two specimens (AMNH 57511–12) collected during the Second Archbold Expedition in 1936, and constituted the first record of *U. preussi* from the southern versant of New Guinea's mountainous spine.

The McDowell revisions (1967–69)

In 1967 herpetologist Samuel Booker McDowell (1928–2014) published a paper on the New Guinea elapid genus *Aspidomorphus* and related genera (McDowell, 1967). In this paper he synonymised *Apistocalamus loennbergii* with *A. loriae*, and *Pseudopistocalamus nymani* with *A. pratti*. He also listed three undescribed species of *Apistocalamus*: Species I from Rossel Island, Species II from Garaina, and Species III from near Okapa, as well as an undescribed species of *Toxicocalamus* from Misima Island. Two years later he published his extensive revision of this group of elapid genera (McDowell, 1969), which included important taxonomic decisions. He reduced *Apistocalamus* and *Ultrocalamus* in taxonomic rank to subgenera of *Toxicocalamus*, as predicted by Boulenger 61 years earlier, he placed *A. pratti* and *A. lamingtoni* into the synonymy of *Toxicocalamus* (*Apistocalamus*) *loriae*, and he removed *Toxicocalamus* (*Ultrocalamus*) *buergersi* from the synonymy of *U. preussi*. In addition, he formally described three of the species he had mentioned in his 1967 work as new, including

Toxicocalamus (*Apistocalamus*) *spilolepidotus* from a single female (AMNH 85745), collected at Purosa (Figure 1, Locality 15), in what is now Eastern Highlands Province, PNG, during the Sixth Archbold Expedition; *Toxicocalamus* (*Apistocalamus*) *holopelturus*, from a single male (AMNH 76660), collected on Rossel Island (Figure 1, Locality 6), Milne Bay Province, PNG, during the Fifth Archbold Expedition; and *Toxicocalamus* (*Toxicocalamus*) *misimae*, from a single male (AMNH 76684), collected on Misima Island (Figure 1, Locality 10) in Milne Bay Province, PNG, also collected during the Fifth Archbold Expedition. He considered the Garaina population, his Species II of 1967, to be a hybrid between *T. loriae* and *T. stanleyanus*.

A new century (2009–present)

In 2009 Fred Kraus described two new species of *Toxicocalamus*, without subgeneric designations (Kraus, 2009). *Toxicocalamus mintoni* was described from the holotype (BPBM 20822), a male collected by John Slapcincky in 2004, on Sudest Island (Figure 1, Locality 9), the third island in the Louisiade Archipelago[7] with an endemic *Toxicocalamus*, while the holotype of *T. pachysomus* (BPBM 15771), also a male, was collected by Kraus in the Cloudy Mountains (Figure 1, Locality 12) of mainland Milne Bay Province in 2002.

The largest member of the genus, *T. ernstmayri* was described by O'Shea et al. (2015). The only known specimen is the holotype, a female (MCZ R-145946) collected

[7] Woodlark Island, a fourth Milne Bay island with an endemic *Toxicocalamus*, is not part of the Louisiade Archipelago but it has strong links with Misima, Sudest, and Rossel Islands. Woodlark Island lies on a ridge known as the Woodlark Terrane, on the northern edge of the submarine Woodlark Basin, while the Louisiade Archipelago lies on the southern edge of the basin, at the eastern end of the Owen Stanley Terrane. Prior to the north–south expansion of the Woodlark Basin, which began in the Pliocene (5–2 MYA), Woodlark Island would have been located much closer to the Louisiade Archipelago than its present isolated position would suggest (Pigram and Davies, 1987).

by then-*kiap*[8] Fred Parker at Wangbin (Figure 1, Locality 4) in the Star Mountains of Western Province, PNG, in late 1969 (O'Shea et al., 2015). However, a live individual was recently observed and photographed at the Ok Tedi Mine, ca. 13 km distant (by air) from the type locality, revealing the body colouration of this species to be a stunning yellow (O'Shea et al., 2018). In late 2017, Fred Kraus described two additional species of *Toxicocalamus* (Kraus, 2017). *Toxicocalamus nigrescens* was described based on a female holotype (BPBM 16545) and an immature paratype (BPBM 16544), collected by P. Robert and Fred Kraus, respectively, on Fergusson Island (Figure 1, locality 11) in the d'Entrecasteaux Archipelago of Milne Bay Province, PNG. In the same paper Kraus described *T. cratermontanus* based on a female holotype (USNM 562941), collected by David Bickford in the Crater Mountain Wildlife Management Area, Simbu Province, central montane PNG (Figure 1, Locality 3). It is certain that further species of *Toxicocalamus* await discovery and description, and several descriptions are already in preparation (Chris C. Austin, *pers. comm.*; O'Shea and Kaiser, *in prep*.).

Materials and Methods

The holotype was collected under applicable permits, fixed using a 10% buffered formalin solution, and subsequently transferred to 70% ethanol for permanent storage. Characters used for evaluating and comparing specimens were taken from 489 museum specimens of *Toxicocalamus* (Supplementary Data: Appendix 1) and 93 specimens of three additional species (Supplementary Data: Appendix 2). Abbreviations for measurements and scale counts used in the description include snout–vent length (SVL), tail length (TL), total length (TTL), number of ventral scales (V), number of subcaudal scales (SC), and number of infralabial scales (IL). Scales were counted as suggested by McDowell (1969). Sex

[8] *Kiap*, a Pidgin word derived from the German *Kapitän*, was applied to Government Patrol Officers during the Australian Administration of what is now Papua New Guinea, which ended with the country's independence in 1975.

was determined by examination of gonads, presence of everted hemipenes, or presence of the *retractor penis magnus* muscle. Length measurements were taken by running a non-elastic string from the tip of the snout along the ventral medial axis of the body, under consideration of the points about measurement accuracy raised by Natusch and Shine (2012). Measurements of tail tips were taken using Mitutoyo digital callipers to the nearest 0.1 mm. X-rays of the holotype were taken using a Kevex PXS5-724EA emitter and a Varian PanScan 4030R receiver (40 kV target tube voltage) at the Museum Support Center of the U.S. National Museum of Natural History, Smithsonian Institution, Suitland, Maryland, USA. For our assessment of colouration, both in life and in preservative, we used the colour guide of Köhler (2012). GPS coordinates were determined using individual museum records and published species accounts where available; those unavailable were obtained from Google Earth (WGS 84) to the nearest minute. Museum acronyms are taken from Sabaj (2016), with the addition of UPSZ, now the preferred acronym for the Museum of Evolution containing the Uppsala University natural history collection (Hans Mejlon, *pers. comm*.).

Results

Toxicocalamus pumehanae sp. n.

(*figs. 3, 4, 7, 8A, 9A*)

Proposed English name: Managalas Plateau Snake

Holotype: BPBM 36185 (Figures 2, 3), a juvenile female from Jarefa Camp village (09°12'19" S, 148°14'15" E; Figure 4), elevation 820 m, near Itokama (= Itogama), on the Managalas Plateau, Managalas Conservation Area, Ijvitari District, Oro Province, Papua New Guinea, collected by Allen Allison in March 2010.

Diagnosis: *Toxicocalamus pumehanae* is only known from its holotype, a diminutive female specimen measuring 220 mm SVL + 21 mm TL = 241 mm TTL. It can be distinguished from all other known *Toxicocalamus* by the following combination of characters: dorsum of head exhibiting fused prefrontal-internasal scutes but separate and distinct single preoculars (an extremely rare combination in Papuan

elapids – see Discussion: Head Scute Fusion); undivided nasal scutes with small, central, circular nares; rostral as broad as high; paired postoculars; single anterior and paired posterior temporals; broad frontal between supraoculars; elongate paired parietals (Figure 5A'), six supralabials, with the 3rd–4th supralabials contacting the orbit (Figure 5C', D'); six infralabials with 1st–3rd contacting anterior genials, anterior genials overlapping, mental groove absent, posterior genials separated by two intergenials, anteriormost on midline, posterior to anterior genials; distinctive dark spot present on junction of 3rd–4th infralabials (Figure 5B'); dorsal scales in 15-15-15 rows; 235 ventrals, followed by a pair of precloacal scales (Figure 5E'); paired cloacal scales; 35 subcaudals, all paired; short tail, laterally slightly compressed, terminating in a conical terminal scale (Figures 5F', 7A).

Comparisons: The genus *Toxicocalamus* can be distinguished from all other terrestrial New Guinea elapid genera, except *Pseudonaja*, by the absence of a temporolabial scale between the 5th and 6th supralabials (see Discussion). Although *Pseudonaja* also lacks a temporolabial scale, it is easily distinguished from *Toxicocalamus* by its large eyes (diameter 1.5 times the distance from the lower edge of the orbit to the margin of the lip), strongly pronounced, protruding supraocular scales, and highly alert and active terrestrial habitus. In contrast *Toxicocalamus* species possess relatively small eyes (diameter subequal to the distance from the lower edge of the orbit to the margin of the upper lip), supraocular scales that do not protrude laterally above the eyes, and they exhibit a secretive, semi-fossorial to terrestrial habitus.

McDowell (1969) synonymised *Toxicocalamus, Apistocalamus*, and *Ultrocalamus* with *Toxicocalamus* and proposed their status as subgenera. The species in the subgenus *Toxicocalamus* (*T. grandis*, *T. holopelturus*, *T. loriae*, *T. spilolepidotus*) exhibit the classic ‘colubrid-elapid nine-scute arrangement’ (sensu O'Shea, 2005:12),

315 as do three recently described species: *T. pachysomus* Kraus, 2009, *T. ernstmayri*
316 O'Shea et al., 2015, and *T. nigrescens* Kraus, 2017. In contrast, species in the subgenera
317 *Apistocalamus* (*T. longissimus*, *T. misimae*, *T. stanleyanus*) and *Ultrocalamus* (*T.*
318 *buergersi*, *T. preussi*) are characterised by some degree of head-scute fusion (Table 1)
319 involving fused preocular-prefrontal scutes in *Apistocalamus,* and fused preocular-
320 prefrontal-internasal scutes in *Ultrocalamus*. The recently described *T. mintoni* Kraus,
321 2015 and *T. cratermontanus* Kraus, 2017 also exhibit fused preocular-prefrontal scutes,
322 although the former is unique in the possession of a head-wide mid-dorsal scute
323 comprising the frontal and both supraocular scutes. *Toxicocalamus pumehamae*
324 exhibits head scute fusion but does not feature any of the hitherto seen *Toxicocalamus*
325 arrangements.

326 We here compare *T. pumehanae* with fifteen congeners (fourteen species and one
327 subspecies), with relevant characteristics for these species presented in parentheses. We
328 also present a listing of these comparative characters, expanded from the version in
329 O'Shea et al. (2015) to include *T. pumehanae* and the recently described *T. nigrescens*
330 and *T. cratermontanu*s (Table 2). *Toxicocalamus pumehanae* exhibits fusion of the
331 prefrontal and internasal scutes (Figures 5A', 8A) that distinguishes it from those
332 species that exhibit the regular 'colubrid-elapid nine-scute dorsal arrangement' (*T.*
333 *ernstmayri*, *T. grandis*, *T. holopelturus*, *T. loriae*[9], *T. nigrescens, T. pachysomus, T.*
334 *spilolepidotus*). Fusion of the prefrontal and internasal scutes without involvement of
335 the preocular scale distinguishes *T. pumehanae* (Figures 5A', C', D', 6A) from *T.*
336 *cratermontanus, T. longissimus*, *T. misimae*, *T. stanleyanus*, and *T. mintoni* (Figures
337 6E–H, fused prefrontal-preocular scutes, but distinct and separate internasal scutes),
338 and from *T. buergersi*, *T. p. preussi,* and *T. p. angusticinctus* (Figures 6B–D, fused

[9] See Discussion: Head Scute Fusion.

339 preocular-prefrontal-internasal scutes). *Toxicocalamus mintoni* further exhibits a broad,
340 head-wide, mid-dorsal scute derived from the fusion of the frontal scute with its
341 neighbouring supraocular scutes (Figure 6E), a character not seen in any other
342 terrestrial elapid, and possibly unique amongst colubroid snakes. The presence of six
343 supralabials separates *T. pumehanae* from *T. p. preussi*, *T. p. angusticinctus*, and *T.*
344 *stanleyanus* (Figures 6C–D, G, five supralabials), and *T. buergersi* (Figure 6B, four
345 supralabials).

346 *Toxicocalamus pumehanae* exhibits a dorsal scale count of 15-15-15 that
347 distinguishes it from *T. p. preussi, T. p. angusticinctus* (both 13-13-13), and *T.*
348 *longissimus* (17-17-17), while the paired cloacal scales separate it from *T. buergersi*, *T.*
349 *cratermontanus, T. preussi*, *T. stanleyanus*, and some Oro Province *T. loriae sensu*
350 *lato*[10] (single cloacal scale), and the mostly paired subcaudal scales separate it from *T.*
351 *holopelturus* (all subcaudals single). However, the regularly formed and paired
352 precloacal scales (Figure 5E') present in the holotype of *T. pumehanae* appear to be a
353 unique character within the genus *Toxicocalamus*, distinguishing it from all other
354 known species, although occasional specimens of *T. loriae* also exhibit irregular,
355 partially or completely paired terminal ventral scutes.

356 The ventral scale count of *T. pumehanae* at 235 is considerably lower than that of
357 female *T. buergersi* (313–319), *T. cratermontanus* (281), *T. holopelturus* (246–256), *T.*
358 *longissimus* (273–304), *T. misimae* (254), *T. p. preussi* (291–331), and *T. p.*
359 *angusticinctus* (345–359), but higher than that of female *T. nigrescens* (193), *T.*

[10] Based on morphological evidence (unpubl. data), the recent analysis by Strickland et al. (2016), and a discordant geographic distribution of available specimens, it is certain that *T. loriae*, as currently defined, is a species complex. This is a key reason why the range of relative tail length values shown in the comparisons and Table 2 is considerably larger than for any other species in the genus. We here refer to specimens of uncertain species affinity, but currently treated as belonging to *T. loriae*, as *T. loriae sensu lato*.

spilolepidotus (200–215), *T. ernstmayri* (203), and *T. grandis* (207). The only species with a female ventral count overlapping that of *T. pumehanae* is *T. stanleyanus* (230–281). The subcaudal scale count of 35 is higher than those of female *T. p. preussi* (16–25), *T. cratermontanus* (25), *T. stanleyanus* (22–29), *T. buergersi* (24–28), *T. longissimus* (24–32), *T. p. angusticinctus* (26–30), *T. grandis* (27), *T. ernstmayri* (29), *T. misimae* (29), and *T. spilolepidotus* (33), lower than the recorded range for female *T. holopelturus* (37–41), but within the range recorded for female *T. loriae sensu lato* (23–38), and the same as the only known female *T. nigrescens* (35). *Toxicocalamus mintoni* and *T. pachysomus* are known only from their male holotypes, both with incomplete tails.

Toxicocalamus pumehanae possesses a moderately long tail (TL/TTL = 8.7%) for a *Toxicocalamus*, with females of other *Toxicocalamus* species possessing much shorter tails, relative to total length (Table 2): *T. p. preussi* (3.9–6.1%), *T. p. angusticinctus* (3.5–8.4%), *T. buergersi* (4.1–6.3%), *T. longissimus* (5.3–7.7%), *T. cratermontanus* (5.6%), *T. misimae* (7.5%), *T. grandis* (7.7%), and *T. ernstmayri* (8.3%). Its relative tail length falls within the ranges of *T. loriae sensu lato* (6.5–15.6%), *T. holopelturus* (7.9–9.2%), and *T. stanleyanus* (5.1–9.7%), but below that of *T. spilolepidotus* (9.4–10.7%), and *T. nigrescens* (11.7%).

The general habitus of *T. pumehanae* is that of a relatively slender, almost petite snake with a head only slightly broader that the body, and almost indistinct from the neck, and a slightly compressed tail that terminates abruptly in a conical tip. This body form contrasts with the more stout-bodied species (*T. grandis*, *T. ernstmayri*, *T. pachysomus*). The body form of *T. pumehanae* appears to lie between that of the more slender *T. loriae sensu lato* and the elongate species in McDowell's subgenus *Ultrocalamus* (*T. buergersi*, *T. p. preussi*, *T. p. angusticinctus*), although it does not

385 exhibit the etiolated body shape of these ultra-slender, “bootlace” species. Any
386 prediction for specific adult body and head proportions would likely be unreliable given
387 that the holotype is a juvenile.

388 *Description of the holotype*: A juvenile female (SVL 220 mm, TL 21 mm, TTL 241
389 mm; Figures 2, 3), with 15-15-15 dorsal scale rows, scales imbricate, all smooth, 235
390 entire ventrals followed by paired precloacal scales, paired cloacal scales, and 35 paired
391 subcaudals. The head measures 5.0 mm long, from front of rostral to posterior of
392 parietal suture, and 4.5 mm wide, across the broadest part of the head in line with the
393 suture between the 5th and 6th supralabials. Eye small, width subequal to vertical
394 distance between eye and lip, along suture between 3rd and 4th supralabials, almost half
395 the distance from orbit to naris. Head exhibits fused prefrontal-internasals, in broad
396 contact (Figure 5A'). Rostral as broad as high, clearly visible from above. Frontal
397 shield-shaped, slightly longer than wide due to a backward projection between the
398 parietals, only slightly larger than the fused prefrontal-internasals. Supraoculars
399 relatively small and discrete. Parietals, paired, angular, 1.6 times as long as broad. Six
400 supralabials, the 3rd and 4th in contact with the orbit (Figure 5C', D'), the 6th being the
401 largest. Nasal large, entire without suture, almost circular except where slightly
402 indented by 1st supralabial, with a round, countersunk, central naris. Nasal in broad
403 contact with a single elongate preocular, preventing contact between the 2nd supralabial
404 and the prefrontal. Loreal absent, as in all elapids; subocular absent, as in all terrestrial
405 Papuan elapid genera except *Acanthophis*; temporolabial absent, in contrast to
406 terrestrial Papuan elapid genera, except congenerics and *Pseudonaja textilis*. A pair of
407 subequal postoculars on either side, in contact with a single elongate anterior temporal
408 that extends backwards to approximately twice its width, to contact the 5th and 6th
409 supralabials, the parietal, and paired posterior temporals. Mental triangular, six

410 infralabials (IL) with $IL^{1–4}$ contacting pregenials (Figure 5B'). Pregenials longer than
411 wide, in broad contact, imbricate, mental groove absent, postgenials longer than wide,
412 separated by an intergenial, smaller than pre- or postgenials.
413 Scales of body rounded, imbricate, smooth, arranged in 15 rows throughout without
414 posterior reduction, and without enlargement of scales in either the 1st or the mid-
415 vertebral rows; dorsal scales of tail as body in seven rows, reducing to five posteriorly.
416 Ventral scales broad, 235 between intergenial and precloacal scales; precloacals paired,
417 with left precloacal overlapping the right (Figure 5E'); cloacal scales paired with the
418 left cloacal overlapping the right; subcaudal scales all paired; tail terminating in a blunt,
419 conical scale (Figure 5F').
420 *Colouration in life* (Figure 2): Dorsum of body and tail glossy Cyanine Blue (189),
421 fading to pale Dark Blue Grey (194) on the lower flanks and venter. Supralabials Pale
422 Horn Color (11) with pigment extending anteriorly onto the nasals, preoculars, and
423 fused prefrontal-internasals, and posteriorly to contact the anterior temporal and the
424 first two scales of the neck, but not contacting the orbit, which is surrounded by Dusky
425 Brown (285) pigment. The tail terminates in a Pale Buff (1) conical tip.
426 *Colouration in preservative*: The dorsum of body and tail are glossy Raw Umber
427 (280) with lighter areas of Medium Blue Grey (193) (Figure 3A). The venter is Flax
428 Flower Blue (196) (Figure 3B). The head is Medium Blue Gray (193) above (Figure
429 5A), Smokey White (261) below, the light pigment extending posteriorly onto the
430 anteriormost ventrals and sometimes reaching the lowest row of dorsal scales (Figure
431 5B). Patterning on the head comprises a broad upwards extension of Smokey White
432 (261) pigment, from the rostral through the 1st–3rd supralabials through the nasal, and
433 preocular, onto the prefrontal-internasal scutes, extending posteriorly through the 4th–
434 6th supralabials but not reaching the upper sutures, resulting in the eye being ringed by

435 Plumbeous (295) pigment (Figure 5C–D). Distinctive twin, Vandyke Brown (281)
436 spots present posterior to the suture between the 3rd and 4th infralabials (Figure 5B).
437 Conical tail tip Smokey White (261), contrasting the colouration of the tail (Figure 5F).
438 *Tail tip morphology*: The tail of *Toxicocalamus pumehanae* is nearly round in lateral
439 cross-section proximal to the cloaca, but becomes laterally compressed distally. The
440 tail ends in a rounded, conical terminal cap (Figure 7A). Internally, the ten terminal
441 vertebrae show no compression and all have approximately the same dimensions
442 (Figure 8A). The tail terminates without ornamentations or any other ossified feature.
443 *Skull morphology*: The skull of *Toxicocalamus pumehanae* (Figure 9A) is elongated
444 (ratio of width at the level of the prootics to length from tip of the anterior surface of
445 the nasal to the right occipital condyle = 0.41) and quite robust. There are six grooved
446 maxillary teeth in a 2 + 4 arrangement, with no diastema between them. The most
447 noteworthy features in terms of differentiating the skull of *T. pumehanae* from that of
448 other species include the reduced anterior extent of the parasphenoid, termination of
449 the palatine tooth row at the anterior level of the parasphenoid, extent and shape of the
450 premaxilla, shape and size of the prootics, extent and shape of the exoccipitals and
451 occipital condyles, and features of the atlas-axis complex (see comparisons below).
452 *Habitat and natural history*: The holotype was collected from within leaf litter in
453 primary rainforest in the vicinity of a small stream, at the base of a gentle slope. The
454 leaf litter was 10–15 cm deep and was covered in a profusion of ground herbs (Figure
455 10 in Supplementary Materials). The individual was found at night, possibly while
456 foraging in the leaf litter, although other species of *Toxicocalamus* are known to be
457 diurnal in activity (O'Shea et al., 2018).
458 The holotype did not contain any gut contents, but snakes in the genus
459 *Toxicocalamus* are believed to be primarily vermivorous (Shine and Keogh, 1996),

460 feeding primarily or exclusively on giant earthworms of the family Megascolecidae.
461 Earthworms or earthworm fragments have been found in the guts of *T. ernstmayri*
462 (MCZ R-145946), *T. loriae* (AMNH R-75336–38, 75341, 75347, 82332; BPBM
463 10967; CAS 121220; MCZ R-111785), *T. pachysomus* (BPBM 15771), and *T. misimae*
464 (SAMA R69921). A specimen of *T. longissimus* collected alive for venom extraction,
465 was induced to feed on earthworms in captivity (Owen Paivu, *pers. comm.*). O'Shea et
466 al. (2015) discussed *Toxicocalamus* prey preferences in greater detail.
467 In common with all other terrestrial Papuan elapids, except *Acanthophis*, snakes of the
468 genus *Toxicocalamus* are believed to be oviparous. Females of *T. loriae sensu lato* have
469 been found to contain thick-shelled oviductal eggs, with clutch sizes ranging from one
470 to eight (Shine and Keogh, 1996). Based on our own observations while examining
471 specimens, we can report on a specimen of *Apistocalamus loennbergi,* a synonym of *T.*
472 *loriae* (MCZ R-119027), and the holotype of *T. spilolepidotus* (AMNH R-85745),
473 which both contained seven eggs.
474 *Distribution and cohabiting snake species*: The species is known only from the type
475 locality, whose snake fauna has not been described in any detail. We have collected
476 museum records to present a brief listing of elapid and non-elapid species known from
477 the type locality and its surrounds. It is not possible to derive any ecological
478 relationships from such a listing, yet it would appear that a significant amount of niche
479 partitioning must exist to accommodate this level if diversity (e.g., Luiselli, 2006).
480 At least 15 other *Toxicocalamus* specimens have been collected in Oro Province but
481 none remotely resemble BPBM 36185, all exhibiting the typical 'colubrid-elapid dorsal
482 nine-scute arrangement' in their head scalation. The type locality of *T. pumehanae* is
483 located less than 10 km from where four *Toxicocalamus loriae sensu lato* (BPBM
484 43027–29, 43032) were collected. Other elapids collected in the local vicinity include

485 both *Aspidomorphus muelleri* (e.g., BPBM 36168) and *Micropechis ikaheka* (e.g.,
486 BPBM 36146). For a more complete list of locally occurring elapids, see Appendix 2
487 in the Supplementary Data file.

488 The non-elapids recorded from the Itokama area include *Indotyphlops braminus*
489 (e.g., BPBM 36170), *Ramphotyphlops* sp. (e.g., BPBM unregistered [AA 19781]),
490 *Gerrhopilus inornatus* (MCZ R-140724), *Candoia aspera schmidti* (BPBM 42995–
491 300), *C. paulsoni mcdowelli* (e.g., BPBM 43006–08), *Candoia* sp. (BPBM unregistered
492 [AA 19781]), *Morelia viridis* (e.g., BPBM 36182–83), *Simalia amethistina* (BPBM
493 43013), *Boiga irregularis* (e.g., BPBM 43001–04); *Dendrelaphis* sp. (e.g., BPBM
494 36186), *Stegonotus* sp. (e.g., BPBM 36142), *Tropidonophis multiscutellatus* (MCZ R-
495 139414), and *Tropidonophis* sp. (e.g., BPBM 36167). For a more complete list of
496 locally occurring non-elapids, see Appendix 3 in the Supplementary Data file.

497 *Etymology*: The species name *pumehanae* is a matronym honouring Kathleen
498 Imada, whose Hawaiian name is Pumehana and who was a collection technician in the
499 Vertebrate Zoology Collection at the Bernice P. Bishop Museum in Honolulu, Hawaii,
500 USA. She was instrumental in the development of the Museum's herpetology
501 collections database and the scientific success of the collection over more than a decade
502 of service. She now works in the Museum's Botany Collection. Most relevant to this
503 paper and this new species is that Pumehana facilitated the visit by MOS to the
504 collection in June 2014 so that he could examine New Guinea elapids; she also arranged
505 a loan of 16 specimens, including the holotype, for further study at the University of
506 Wolverhampton (United Kingdom), in late 2014.

507

508 **Discussion**

Toxicocalamus pumehanae may be distinguished from other members of genus *Toxicocalamus* by a combination of characteristics, some of which it shares with congeners, while others are unique. Following the comments on the taxonomic history of the entire genus, we here comment on the characteristics that we have generally found useful in distinguishing species of *Toxicocalamus* from congeners as well as from other snakes, especially with a view to identification in the field. These include (1) colour pattern of the head; (2) fusion of several head scutes in diverse patterns; (3) size and position of the nares in the nasal scute; (4) number of supralabials, with or without the presence of a temporolabial scale (the absence of which is diagnostic for *Toxicocalamus* and *Pseudonaja* amongst terrestrial Papuan elapids); (5) number of dorsal scale rows; (6) general body physique; (7) number of ventral scales; (8) condition of the cloacal scales and the presence or absence of a pair of precloacal scales; (9) number of subcaudals, paired or unpaired; and (10) tail morphology.

Dorsal head colouration

The holotype of *T. pumehanae* exhibits a head colour pattern previously not seen in any congener, particularly with regards to the juxtaposition of light and dark areas along the mouth. Varying degrees of head banding or barring are present in many juvenile specimens of *T. loriae* sensu lato, *T. stanleyanus*, and *T. preussi* and, although they usually appear as complete nuchal or anterior crossbands, they appear to be ontogenetic characteristics that disappear or become less distinct with age. The most characteristic marking on the head of the juvenile holotype of *T. pumehanae* is the presence of a pair of relatively large dark spots (Vandyke Brown) posterior to the sutures between the 3rd–4th infralabials. The marking has not been observed in juveniles of any other *Toxicocalamus* species.

534

535 *Head scute fusion*

536 Most terrestrial Australo-Papuan elapids exhibit the classic 'colubrid-elapid dorsal
537 nine-scute arrangement,' comprising distinct and separate paired internasal scutes (IN),
538 paired prefrontal scutes (PF), a central, frontal scute (F), bordered on either side by a
539 single supraocular scute (SO), and posteriorly by a pair of parietal scutes. Laterally,
540 between the rostral and the orbit, the head scutes comprise a nasal scute, containing the
541 naris, and usually a single preocular scute, with all elapids lacking a loreal scute.

542 Any changes to this arrangement, through fusion of various scutes, may be
543 considered as the derived character state (Marx and Rabb, 1970; 1972). These authors
544 referred to the 'colubrid-elapid dorsal nine-scute arrangement' as State I and reported
545 that it occurs in 836 of 1003 species (83.4%) and 163 of 201 genera (81.1%), in the
546 Colubridae (sensu lato), and 138 of 139 species (99.3%) and 28 of 29 genera (96.6%)
547 in the terrestrial Elapidae[11]. They referred to any fusion of dorsal head scutes resulting
548 in fewer than nine dorsal scutes as State IV and reported this condition in 98 of 1003
549 species (9.8%), 26 of 201 genera (12.9%) in the Colubridae (sensu lato), and one of 129
550 species (0.7%) and one of 29 genera (3.4%) in the terrestrial Elapidae, reporting that
551 "State IV is present only in the monotypic genus *Ultrocalamus*."

552 Marx and Rabb (1970) reported that in the colubrids (sensu lato) State IV is restricted
553 to aquatic, secretive fossorial, and subterrestrial snakes, which was also said to hold
554 true for elapids. In fossorial species they proposed that fusion of the head scutes serves
555 to strengthen the head, which is used as a "blunt instrument" for subterranean
556 burrowing, as exemplified by the fusion of head scutes in the colubrid genus *Calamaria*
557 (Inger and Marx, 1965), a genus possibly convergent with *Toxicocalamus*.

[11] The authors recognized Hydrophiidae for all marine elapids, *fide* Smith (1926).

558 Head scute fusion is actually present in a greater number of Australo-Papuan elapids
559 than was recognized by (Marx and Rabb, 1970; 1972), including 53% of all known
560 *Toxicocalamus* species (Figure 6), but fusion of the prefrontal and internasal scutes has
561 only been recorded in the subgenus *Ultrocalamus* (*T. preussi* and *T. buergersi*), and
562 then only in combination with the preocular scute, to form a pair of expansive anterior
563 dorsal head scutes. These two taxa, which exhibit the greatest degree of head scute
564 fusion, may also be the most fossorial species in the genus, thereby supporting the
565 above hypothesis of Marx and Rabb (1970). The members of the subgenus
566 *Toxicocalamus* (*T. longissimus, T misimae*, and *T. stanleyanus*), together with *T.*
567 *mintoni*, exhibit fusion of the preocular and prefrontal scutes, but retain distinct and
568 separate internasals.
569 Greer (1997) also recorded fusion of the prefrontal and internasal scutes, without
570 involvement of the preocular scute, as a constant condition in the Australian elapids
571 *Rhinoplocephalus bicolor* and *Vermicella multifasciata,* while Cogger (2014) reported
572 the lack of internasal scutes in *V. intermedia*, whose nasals are in broad contact with
573 the prefrontals on the head. Greer (1997) also recorded fusion of the prefrontal-
574 internasal scutes as an occasional condition in King Island (Bass Strait) tigersnakes,
575 *Notechis ater humphreysi*, now *N. scutatus humphreysi*[12]*,* but he did not specify via
576 citation or listing which specimens exhibited this condition. However, Mirtschin and
577 Davis (1982:95) include line drawings of a specimen of "*Notechis a. humphreysi*" with
578 partially but irregularly fused prefrontal and internasal scutes, clearly an aberrant
579 condition in this taxon.

[12] Some authorities only recognise two subspecies, *Notechis s. scutatus* from southern and southeastern Australia, and *N. s. occidentalis* from southwestern Australia (Uetz et al., 2018), but other authors still recognise all six former subspecies of *Notechis ater* and *N. scutatus*, as subspecies of *N. scutatus* (Cogger, 2014; Mirtschin et al., 2017; Wilson and Swan, 2017)

McDowell (1967) also documented fusion of the prefrontal and internasal scutes as an occasional condition in *Aspidomorphus schlegelii* in New Guinea. He examined four specimens of *A. schlegelii*, three from West Papua Province, WNG (BPBM 5133, MCZ R-7311, R-38967), and one from Papua Province, WNG (MCZ R-7080). This last specimen exhibits incomplete and irregular fusion of the prefrontal and internasal scutes on the left side, and while the scutes on the right side are separate, the right internasal is itself further divided by a partial suture. This is also the specimen listed by Barbour (1908) as the holotype of *Pseudelaps muelleri insulae*, but without drawing attention to the head scute fusion in his description. We examined McDowell's four specimens, and a further 80 specimens of *A. schlegelii,* from across the taxon's entire range, from Sandaun Province (PNG), and Papua and West Papua Provinces (WNG), including the Schouten Islands (Yapen, Biak, and Numfoor), and Djamna Island (Papua Province), and Mansinam Island and the Raja Ampat Archipelago (Salawati, Batanta, Waigeo and Misool; all West Papua Province). Apart from the Djamna Island specimen, all exhibited the "colubrid-elapid dorsal nine-scute arrangement." We have also located a single adult female specimen (AM R.14788, SVL 588 mm) of *Toxicocalamus loriae sensu lato*, part of a series of five specimens (MCZ R-14783, 14785–88) collected by Fred Parker at Kimil, Jiwaka Province, in the Wahgi Valley (PNG), that exhibits a pair of perfectly formed, fused prefrontal-internasal scutes[13]. None of its conspecifics, nor any of the other, approximately 170 specimens of *T. loriae sensu lato* collected in the Wahgi Valley exhibit this condition, so we consider it an aberrant condition in that individual. Given that Kimil is located 565 km NW of the type locality of *T. pumehanae* we do not believe that this one character of MCZ R-14788 indicates any relationship to the new taxon.

[13] AM R.14788 also exhibits paired cloacal scales, the normal condition, and a partially divided terminal ventral scale, with a small median scale extending forwards onto the paired cloacal scales.

The complete and regular fusion of the prefrontal with the internasal, without involvement of the preocular, in *T. pumehanae*, would therefore appear to be a unique, species-specific character within the genus *Toxicocalamus*.

Naris and nasal arrangement

Most species of *Toxicocalamus* possess moderately large and irregularly circular nares, with at least a lower suture partially dividing the nasal scute. The nares of *T. pumehanae* are very small, perfectly rounded, and countersunk in the centre of the nasal scutes, with only the faintest evidence of a lower nasal suture. This condition is also observed in the subgenus *Ultrocalamus* in *T.* (*U.*) *buergersi* and *T.* (*U.*) *preussi*.

Number of supralabials

All species of *Toxicocalamus* lack a temporolabial scute and possess six or fewer supralabials. Other than in *T. pumehanae*, six supralabials are also found in the subgenus *Apistocalamus* (*T. grandis, T. holopelturus, T. loriae*, and *T. spilolepidotus*) and also in *T. ernstmayri, T. nigrescens,* and *T. pachysomus*, all of which exhibit the 'colubrid-elapid dorsal nine-scute arrangement.' It is also found in the subgenus *Toxicocalamus* (*T. longissimus,* and *T. misimae*) and *T. mintoni*, which exhibit fusion of the preocular and prefrontal scutes, but possess distinct and separate internasals. The *Ultrocalamus* taxa (*T. preussi* and *T. buergersi*), to which *T. pumehanae* bears a resemblance in other characters, possess five and four supralabials, respectively.

Dorsal scale rows

The count of 15-15-15 is consistent with those of all other *Toxicocalamus*, with the exception of *T. longissimus* (17-17-17) and *T. preussi* (13-13-13).

General body physique

The genus *Toxicocalamus* contains species exhibiting a wide diversity of body physiques. The two members of the subgenus *Ultrocalamus* (*T. buergersi* and *T. preussi*) are extremely etiolated snakes, which we have likened to 'bootlaces', a morphology that reaches its extreme in specimens of *T. preussi angusticinctus* from the Upper Fly of Western Province, PNG. In their extremely slender body shape these *Toxicocalamus* resemble the Southeast Asian "long-glanded coralsnakes" of the genus *Calliophis*, and the resemblance is not confined to their external morphology. *Toxicocalamus buergersi,* at least, possesses extremely long venom glands that extend backwards from the head into the body cavity for almost one-third of the snake's total snout–vent length (McDowell, 1969, O'Shea, pers. obs.). *Toxicocalamus stanleyanus* is also an ultra-slender species resulting in specimens occasionally being mislabelled as *T. preussi*.

At the other end of the scale there are a number of stouter-bodied species (e.g., *T. ernstmayri, T. grandis, T. pachysomus*), whose general physiques are comparable with a great many colubrid or elapid species. The remaining species (*T. holopelturus, T. longissimus, T. loriae, T. mintoni, T. misimae*, *T. spilolepidotus*) exhibit physiques that fall between the bootlace and the stouter-bodied forms.

Often body physique and girth can be directly related to the number of dorsal scale rows (i.e., more scales = greater girth), but whereas *T. preussi* (13-13-13) is very slender, so is the other member of the subgenus *Ultrocalamus*, *T. buergersi* (15-15-15); the species with the highest dorsal count, *T. longissimus* (17-17-17), is actually more slender than the three most robust species, *T. ernstmayri, T. grandis*, and *T. pachysomus* (all 15-15-15).

654 *Toxicocalamus pumehanae* is only known from the single juvenile holotype but it
655 appears to fall into the middle category, neither excessively slender nor robustly stout,
656 though leaning towards *Ultrocalamus* (*T. preussi*, *T. buergersi*) in *gestalt*. Interestingly,
657 the holotype of *T. pumehanae* also contains an elongate venom gland, similar in
658 appearance to that of *T. buergersi*, that extends backwards through the body cavity to
659 at least ventral scale 96 (Figure 3B).
660
661 *Ventral scale count*
662 The female holotype of *T. pumehanae* possesses 235 ventral scales between the
663 intergulars and the paired precloacal scales (see below), a count considerably below the
664 counts for females of the *Ultrocalamus* species with which it bears the strongest
665 resemblance (*T. buergersi*: 313–319; *T. preussi*: 291–359). The only *Toxicocalamus*
666 species with a documented female count close to that of *T. pumehanae* is *T. stanleyanus*
667 (230–281), a species exhibiting fused preocular-prefrontal scutes, separate internasals,
668 and five supralabials.
669
670 *Cloacal and precloacal scales*
671 The holotype of *T. pumehanae* has paired cloacal scales, which is a common feature of
672 other *Toxicocalamus,* but does not occur in *T. buergersi, T. cratermontanus, T. preussi,*
673 *T. stanleyanus,* and Oro specimens of *T. loriae* s.l., previously recognized as *T.*
674 *lamingtoni*. In contrast, the presence of a pair of regularly sized precloacal scales,
675 subequal in size to the paired cloacal scales, appears to be a unique characteristic. There
676 are occasional specimens of *T. loriae* that have some degree of partitioning of the
677 terminal ventral scute, anterior to the cloacal scales, but these look like aberrant divided
678 or partially divided ventral scutes, whereas the precloacal scales of *T. pumehanae* are

679 rounded, regular, and almost exact duplicates of the paired cloacal scales themselves.
680 Such distinctive, paired precloacal scales only exist in one other specimen we have
681 seen, a very distinctive specimen purportedly from Samarai Island, PNG (AM R-5038),
682 which we are describing as a new species (O'Shea & Kaiser, in prep.).
683
684 *Subcaudal scale count and condition*
685 A count of 35 paired subcaudal scales is higher than the subcaudal counts for females
686 of most *Toxicocalamus* species, including the morphologically similar *T. buergersi* and
687 *T. preussi*, lower than the count for *T. holopelturus*, the only species with single
688 subcaudal scales, but it falls within the range *T. loriae* s.l., from which it differs in other
689 important aspects. The only known adult female specimen of *T. nigrescens* exhibits
690 exactly the same subcaudal count as the holotype of *T. pumehanae*. An unsexed
691 immature specimen of *T. nigrescens* exhibits a subcaudal count of 42 (Kraus, 2017),
692 indicating that is it probably a male.
693
694 *Tail tip morphology*
695 The tail of *T. pumehanae* is laterally compressed with a rounded, conical terminal cap
696 (Figure 7A). In this respect it resembles most closely the tails of *T. buergersi* (Figure
697 7B) and *T. preussi* (Figure 7C, D), members of the subgenus *Ultrocalamus*. Other
698 *Toxicocalamus* possess rounded, stouter tails that terminate in a pointed conical scale
699 (e.g., *T. ernstmayri* and *T. grandis*; Figures 7E, F, respectively), or they possess long
700 tails that taper gradually to a pointed terminal spine, (e.g., *T. loriae* s.l., *T. nigrescens,*
701 *T. longissimus, T. holopelturus, T. misimae, T. spilolepidotus, T. stanleyanus,* and *T.*
702 *cratermontanus,* Figures 7G–N, respectively). No other female *Toxicocalamus* has a

703 relatively long tail (35 subcaudals and a TL/TTL radio of 8.7%) with lateral
704 compression and a conical terminal cap.

705 X-ray images of *Toxicocalamus* tail tips (Figure 8) reveal that only the tail tip of *T.*
706 *pumehanae* ends without differentiation among the six terminal vertebrae (Figure 8A).
707 In all other species examined, at least three of the terminal vertebrae are dorsoventrally
708 compressed to some degree, exhibiting a much-diminished size of the terminal vertebra.
709 In addition, the terminus of the tail in *T. ernstmayri* (Figure 8H) has an expanded
710 ossified ornamentation, which is absent in the other species. Furthermore, the gross
711 extent of the vertebral body and processes is relatively small in *T. pumehanae* compared
712 to *T. buergersi*, *T. loriae* (*lamingtoni*), *T. longissimus*, *T. misimae*, and *T. ernstmayri*,
713 bearing similarity only to the tail vertebrae of *T. loriae sensu lato* and *T. grandis*.

714

715 *Skull morphology*

716 The skull of *T. pumehanae* (Figure 9A) can be readily differentiated from the skulls of
717 the other examined species by possessing a unique series of characters. A key feature
718 is the reduced anterior extent of the parasphenoid, which extends anteriorly to only less
719 than one half of the frontal length. In all other species we examined, this bone extends
720 by two thirds or more into the length of the frontal. This relationship between bones is
721 also reflected in the level along the parasphenoid where the palatine tooth row
722 terminates. In *T. pumehanae*, the palatine tooth row ends at the anterior level of the
723 parasphenoid, whereas in all other species examined it extends to one third or more
724 along the length of the parasphenoid. Ossification of the premaxilla is greatly reduced
725 in several species of *Toxicocalamus*, yet in *T. pumehanae* it is reduced to merely a
726 point-sized ossification center. The premaxillary shape is not horizontally flattened
727 anteriorly as in all other examined species, but it protrudes slightly. Unlike in *T.*

728 *buergersi*, *T. longissimus*, *T. loriae sensu lato*, *T. misimae*, *T. grandis*, and *T.*
729 *ernstmayri*, the prootics do not meet dorsomedially. The anterior edge of the prootics
730 is gently curved and the posterior edge nearly straight, which is different from the shape
731 of prootics in the other examined species. The exoccipitals in *T. pumehanae* form
732 pronounced occipital condyles, unlike the weakly protruding occipital condyles seen in
733 *T. loriae* (*lamingtoni*), *T. loriae sensu lato*, *T. longissimus*, *T. misimae,* and *T. grandis*.
734 Lastly, the atlas-axis complex of *T. pumehanae* comprises a relatively robust atlas
735 supported by a strongly built axis relative to the other species.
736
737 *Conclusions*
738 From Rossel Island in the Louisiade Archipelago, Milne Bay Province, PNG, to Fakfak
739 on the Onin Peninsula, WNG, the genus *Toxicocalamus* occurs across a distance of
740 almost 2600 km on the largest tropical island in the world, including many of its satellite
741 archipelagos and islands. With fifteen species (16 taxa) now described, *Toxicocalamus*
742 is by far the most diverse terrestrial elapid genus in Melanesia (the next largest
743 Melanesian genus, *Aspidomorphus*, contains only three species); within the broader
744 Australo-Papuan Region, *Toxicocalamus* is approached only by *Demansia* (currently
745 14 species, 16 taxa). The species number of *Toxicocalamus* is certain to increase in
746 following years, as it is known several colleagues are also working on the descriptions
747 of new taxa (Christopher Austin, *pers. comm*., Fred Kraus, *pers. comm*.), and new
748 molecular tools enable workers to decipher some of the conundrums that exist within
749 the grab-bag taxon *T. loriae* (e.g. Strickland et al., 2016).
750 That such diversity of physique, size, and scalation should exist in so widely
751 distributed a secretive, semi-fossorial or terrestrial Melanesian snake genus, is perhaps
752 not surprising. Although a few species may appear to occupy large ranges (*T. loriae*

753 *sensu lato, T. stanleyanus, T. preussi*), most species exhibit extremely localised
754 endemicity, occurring on individual islands (*T. misimae, T. holopelturus, T. mintoni*)
755 or in remote montane regions (*T. cratermontanus, T. spilolepidotus*).

756 Agriculture in the Highlands of New Guinea is believed to date back 9000 years
757 (Hope et al., 1983), the rich and fertile soil feeding many generations of Papuans, and
758 presumably also supporting a large population of earthworms, with the potential to
759 support a similarly large population of vermivorous snakes – approximately 170
760 specimens of *T. loriae* have been collected in the agriculturally very active Wahgi
761 Valley of Western Highlands, Jiwaka and Simbu Provinces (PNG) alone.

762 Whereas the semi-fossorial/terrestrial leaf-litter niche is occupied by a diverse
763 assemblage of snake genera and species in Asia, Africa, or Latin America, throughout
764 much of its range *Toxicocalamus* occurs in sympatry with only four other ground-
765 dwelling snake genera: the colubrid genus *Stegonotus,* and the elapid genera
766 *Acanthophis*, *Aspidomorphus*, and *Micropechis*. All four of these genera prey primarily
767 on vertebrates. Feeding primarily, if not exclusively, on earthworms, *Toxicocalamus*
768 does not appear to be in competition with any other snake taxa. The only other
769 vermivorous snake genera in western Melanesia are the terrestrial homalopsids of the
770 genus *Calamophis*, which occur on the Vogelkop Peninsula and on the islands of
771 Cenderwasih Bay, WNG (Murphy et al., 2012; O'Shea and Kaiser, 2016), and the
772 typhlopid genus *Acutotyphlops* from the Bismarck Archipelago and Bougainville,
773 PNG, and the Solomon Islands (Wallach, 1995). These areas lie outside the known
774 range of *Toxicocalamus*, and it would therefore appear that the vermivorous snakes of
775 Melanesia occupy mutually exclusive ranges.

776 It is worth noting that whilst the relatively stout-bodied species exhibiting the
777 'colubrid-elapid nine-scute arrangement' (*T. grandis, T. pachysomus*, *T. ernstmayri*),

778 are probably active on the surface during the day (O'Shea et al., *at press*), some of the
779 'bootlace' species (*T. buergersi, T. preussi*) are likely to be more semi-fossorial in
780 habit, possibly even active burrowers. It appears that these extremely etiolated species
781 are less able to survive on the surface, and several specimens of the most slender taxon,
782 *T. preussi angusticinctus*, having been found desiccated and dead on the forest floor
783 (Stephen J. Richards, *pers. comm*.). Since the morphology and ecology of
784 *Toxicocalamus* appears to mirror that of *Calamaria* (Colubridae: Calamarinae: 61
785 species) in Southeast Asia; *Geophis* (Dipsadidae: Dipsadinae: 50 species) in Central
786 America, and *Atractus* (Dipsadidae: Dipsadinae: 143 species) in South America (Uetz
787 et al., 2018), it is probable that we are only beginning to scratch the surface with regards
788 to understanding this genus. The advent of more accurate and affordable molecular
789 techniques, including methods that enable DNA to be sequenced from old museum
790 specimens fixed in formalin, will greatly enhance our ability to determine the true
791 diversity and relationships of *Toxicocalamus*.
792
793 **Revised Key to the Species of *Toxicocalamus***
794 The most recent dichotomous key for the genus *Toxicocalamus* was presented by
795 O'Shea et al. (2015). We here integrate some additional information and build on the
796 earlier keys provided by McDowell (1969), O'Shea (1996), Kraus (2009), and O'Shea
797 et al. (2015) and expand it to incorporate, *T. cratermontanus, T. nigrescens*, and *T.*
798 *pumehanae*.
799
800 1a Preocular scale distinct and separate, not fused with prefrontal scale; always six
801 supralabials; dorsal scales arranged in 15-15-15 scale rows 2

1b Preocular scale fused with prefrontal scale; six or fewer supralabials; dorsal scales always arranged in 13-13-13, 15-15-15, or 17-17-17 scale rows 9

2a Prefrontal and internasal scale fused; nasal scale entire, or only shallowly and incompletely divided, by a small, inferior nasal suture; naris small, round and countersunk in lower centre of nasal scale; paired cloacal scales preceded by a pair of distinct, rounded, subequal precloacal scales; tail laterally compressed, terminating in a conical terminal scale ..... *T. pumehanae*

2b Prefrontal and internasal scales not fused, distinct and separate scales; nasal scale usually divided into anterior and posterior halves by a distinct nasal suture; naris relatively large, irregular in shape, positioned anterior to, or as part of, nasal suture; no paired precloacal scales, or if present resembling a partially divided ventral scale; tail not compressed, but may be slender or stout, with a sharply pointed terminal scale[14] 3

3a Subcaudals entire throughout..... *T. holopelturus*

3b Subcaudals all or mostly divided 4

4a Distinctive patterning, consisting of a yellow central spot on every chocolate scale on head and body, except on the vertebral row; ventral scales yellow with chocolate brown suturing..... *T. spilolepidotus*

4b Patterning not as in 4a.....5

5a Habitus generally slender; adult size < 700 mm TTL; patterning, if present, includes yellow supralabials and frequently a yellow crescent-shaped marking on the nape of the neck, which fades dorsally, and in specimens where it meets mid-dorsally there may also be pale cross bars on the parietal and prefrontal scales *T. loriae sensu lato*

[14] The tail of the only specimen of *T. pachysomus* is truncated, hence it is not known how the tail terminates.

826 5b Habitus robust; adult size > 700 mm TTL; patterning not as above.....6

827 6a Internasal and preocular scales in contact, separating nasal scale from prefrontal

828 scale; head tapering to markedly pointed snout.....*T. pachysomus*

829 6b Internasal and preocular scales not in contact, separated by contact between nasal

830 and prefrontal scales; head rounded, not tapering to pointed snout.....7

831 7a Dorsum of body and tail unicolour black or dark grey; tail relatively long, TL/TTL

832 ration greater than 11%; d'Entrecasteaux Archipelago only

833 .....*T. nigrescens*

834 7b Dorsum of body and tail either brownish with multiple irregular yellowish spots,

835 or with a yellow and black reticulate pattern, tail relatively short, TL/TTL less

836 than 9%; mainland New Guinea 8

837 8a Postocular scale single; point contact only between preocular and nasal scales; 6th

838 supralabial widely separated from upper posterior temporal scale by large anterior

839 temporal scale; patterning irregular, comprising scattered yellow spots on a brown

840 dorsum..... *T. grandis*

841 8b Postocular scales paired; broad contact between preocular and nasal scales; large

842 6th supralabial only narrowly separated from upper posterior temporal scale by

843 narrow anterior temporal scale (posterior temporal scales fused on left side in the

844 holotype); regular patterning comprising grey anterior and yellow posterior to

845 every dorsal scale, presenting a reticulate pattern ..... *T. ernstmayri*

846 9a Cloacal plates paired; always six supralabials.....10

847 9b Cloacal plate single; four or five supralabials.....12

848 10a Dorsal scale rows in 17-17-17 rows..... *T. longissimus*

849 10b Dorsal scales in 15-15-15 rows.....11

11a Supraoculars fused with frontal to form a unique, broad, trans-dorsum head scute between the eyes ..... *T. mintoni*

11b Supraoculars distinct and separate from frontal, three scales across width of head above the eyes ..... *T. misimae*

12a Internasal scale fused with prefrontal and preocular scales to form a single large antero-dorsal scute; anterior temporal scale absent, allowing contact between final supralabial and parietal scale; four or five supralabials 13

12b Internasal scale separate and distinct from fused prefrontal-preocular scute; anterior temporal scale present, preventing contact between 6th supralabial and parietal scale; always five supralabials 15

13a Dorsals scales arranged in 13-13-13 rows; five supralabials; postocular scale always distinct and separate ..... *T. preussi* 14

13b Dorsal scales arranged in 15-15-15 rows; four supralabials; postocular scale fused with supraocular scale ..... *T. buergersi*

14a Five supralabials with 5th supralabial largest, and widely separated from single postocular scale, 4th supralabial in broad contact with parietal scale; males with 280–304 ventrals, 39–54 subcaudals, females with 291–331 ventrals, 16–25 subcaudals ..... *T. preussi preussi*

14b Five supralabials with 5th supralabial largest, and in contact with single postocular scale, preventing contact between 4th supralabial and parietal scale; males with 263–339 ventrals, 38–45 subcaudals, females with 283–359 ventrals, 26–30 subcaudals ..... *T. preussi angusticinctus*

15a Fewer than 172 ventral scales, 5th supralabial taller than broad; pale nuchal band usually present across neck ..... *T. stanleyanus*

874 15b More than 180 ventral scales; 5th supralabial broader than tall; pale patch present
875 on lower neck but not extending across the dorsum ..... *T. cratermontanus*
876

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Table 1. Comparisons between head scute fusion arrangements in the genus *Toxicocalamus*. Scute abbreviations include preocular (PR), prefrontal (PF), internasal (IN), frontal (F), and supraocular (SO). Coloured bars indicate fusion of different sets of scutes. Members of *Toxicocalamus* not included in this table do not exhibit head scute fusion.

Species	**PR**	**PF**	**IN**	**F**	**SO**
T. buergersi					
T. preussi preussi					
T. preussi angusticinctus					
T. longissimus					
T. misimae					
T. stanleyanus					
T. cratermontanus					
T. mintoni					
T. pumehanae sp. nov.					

Table 2. Comparative data for species in the genus *Toxicocalamus*, including *T. pumehanae* sp. nov. Displayed characteristics include the number of specimens examined (*n*) and maximum lengths for males and females. Asterisks (*) denote specimens with an incomplete tail. For missing data, we use the symbol ⊙ when no specimens exist and • where specimens exist but cannot be evaluated for the character (e.g., due to truncated tails). Abbreviations include snout–vent length (SVL), tail length (TL), total length (TTL), frontal (F), internasal (IN), postoculars (PO), prefrontals (PF), preoculars (PR), supralabial (SL), and supraocular (SO).

Character	**Sex**	**Taxon**			
		pumehanae **sp. nov.**	*buergersi*	*cratermontanus*	*ernstmayri*
n		1♀	2♂ 5♀	1♀	1♀
Maximum Known Length (SVL + TL = TTL)	♂	⊙	330 + 35 = 365	⊙	⊙
	♀	220 + 21 = 241	567 + 24 = 591	686 + 41 = 727	1100 + 100 = 1200
Head characters					
Dorsal and dorsolateral head scute, fusion		PF + IN	PF + PR + IN	PF + PR	none
Postoculars, fused with SL, single, or paired		paired	fused	single	paired
Anterior temporal, absent, single, or paired		single	absent	single	single
Posterior temporals, single or paired		paired	single	paired	paired
Supralabials, number (contact orbit)		6 (3+4)	4 (2+3)	5 (2+3)	6 (3+4)
Body characters					
Dorsal scale rows, numbers		15-15-15	15-15-15	15-15-15	15-15-15
Ventrals, number, mean ± SD (Range)	♂	⊙	297 (293–301)	⊙	⊙
	♀	235	319 ± 7.4 (311–330)	281	203
Cloacal scale, single or paired		paired	single	single	paired
Subcaudal scales, single or paired		paired	paired	paired	paired
Subcaudal scale count	♂	⊙	43 (40–46)	⊙	⊙
	♀	35	25 ± 3.6 (20–29)	25	29
Ratio of TL to TTL (%), mean ± SD (Range)	♂	⊙	10.3 (9.6–11.0)	⊙	⊙
	♀	8.7	5.3 ± 0.9 (4.1–6.3)	5.6	8.3
Tail shape and termination		flat, conical	flat, rounded	stout, conical	stout, conical

1061 Table 2 (continued)

Taxon				
grandis	*holopelturus*	*longissimus*	*loriae sensu lato*	*mintoni*
1♀	15♂ 4♀	9♂ 8♀	131♂ 133♀	1♂
⊙	675 + 122 = 797	590 + 75 = 665	655 + 117 = 772	500 + 111 = 611*
960 + 80 = 1040	760 + 77 = 837	715 + 44 = 759	666 + 69 = 735	⊙
none	none	PF + PR	none	PF + PR, SO + F
single	paired	usually single	usually paired	single
single	single	single	single	single
paired	paired	paired	single or paired	paired
6 (3+4)	6 (3+4)	6 (3+4)	6 (3+4)	6 (3+4)
16-15-15	15-15-15	17-17-17	15-15-15	15-15-15
⊙	242 ± 6.0 (226–251)	257 ± 10.3 (244–273)	191 ± 9.7 (160–212)	194
207	252 ± 4.8 (246–256)	285 ± 11.5 (273–304)	204 ± 10.6 (172–232)	⊙
paired	paired	paired	single or paired	paired
paired	single	paired	paired	paired
⊙	60 ± 3.9 (54–68)	47 ± 1.3 (44–48)	44 ± 2.9 (32–54)	51+
27	38 ± 1.9 (37–41)	28 ± 3.1 (24–32)	30 ± 2.8 (23–38)	⊙
⊙	15.7 ± 0.6 (15.0–17.0)	11.5 ± 0.7 (10.4–12.2)	15.9 ± 2.0 (10.8–20.1)	•
7.7	8.8 ± 0.6 (7.9–9.2)	6.2 ± 0.8 (5.3–7.7)	10.2 ± 1.5 (6.5–15.6)	⊙
stout, conical	elongate, conical	elongate, conical	elongate, conical	•

1062

1063

Table 2 (continued).

Taxon				
misimae	*nigrescens*	*pachysomus*	*preussi preussi*	*preussi angusticinctus*
5♂ 1♀	1♀ 1 unsexed[15]	1♂	22♂ 9♀	18♂ 12♀
450 + 70 = 520	⊙	500 + 46 = 546*	690 + 70 = 760	570 + 55 = 625
446 + 36 = 482	635 + 84 = 719	⊙	744 + 40 = 784	900 + 49 = 949

PF + PR	none	none	PF + PR + IN	PF + PR + IN
single or paired	single	single	single	single
single	single or paired	single	absent	absent
paired	paired	paired	single	single
6 (3+4)	6 (3+4)	6 (3+4)	5 (2+3)	5 (2+3)

15-15-15	15-15-15	15-15-15	13-13-13	13-13-13
227 ± 4.6 (219–231)	⊙	171	294 ± 7.1 (280–304)	298 ± 28.3 (231–350)
253	193	⊙	315 ± 11.1 (293–331)	325 ± 35.4 (265–363)
paired	paired	paired	single	single
paired	paired	paired	paired	paired
47 ± 3.0 (42–50)	⊙	20+	45 ± 4.5 (39–54)	41 ± 2.7 (37–48)
29	35	⊙	22 ± 3.2 (16–29)	29 ± 3.4 (22–33)
14.5 ± 1.2 (13.3–16.0)	⊙	•	11.6 ± 1.4 (10.1–14.1)	9.9 ± 1.8 (7.7–15.2)
7.2	11.7	⊙	5.2 ± 1.0 (3.9–6.9)	6.0 ± 1.2 (3.5–7.6)
elongate, conical	elongate, conical	•	flat, rounded	flat, rounded

[15] Gender-relevant data from the unsexed juvenile (such as measurements or counts of ventrals and subcaudals) are not included in the listing, but other characteristics conform to within-species parameters.

1067 Table 2 (continued).

Taxon	
spilolepidotus	*stanleyanus*
2♀	24♂ 19♀
⊙	529 + 83 = 612
770 + 80 = 850	667 + 38 = 705

none	PF + PR
paired	single
single	single
single or paired	paired
6 (3+4)	5 (2+3)

15-15-15	15-15-15
no data	230 ± 8.8 (213–245)
200–205	246 ± 11.0 (230–267)
paired	single
paired	paired
no data	45 ± 4.3 (35–51)
33	25 ± 1.8 (22–29)
no data	13.4 ± 2.7 (9.0–21.1)
10.1 (9.4–10.7)	7.0 ± 1.3 (5.4–9.5)
elongate conical	elongate conical

1068

1069

Figures and Captions

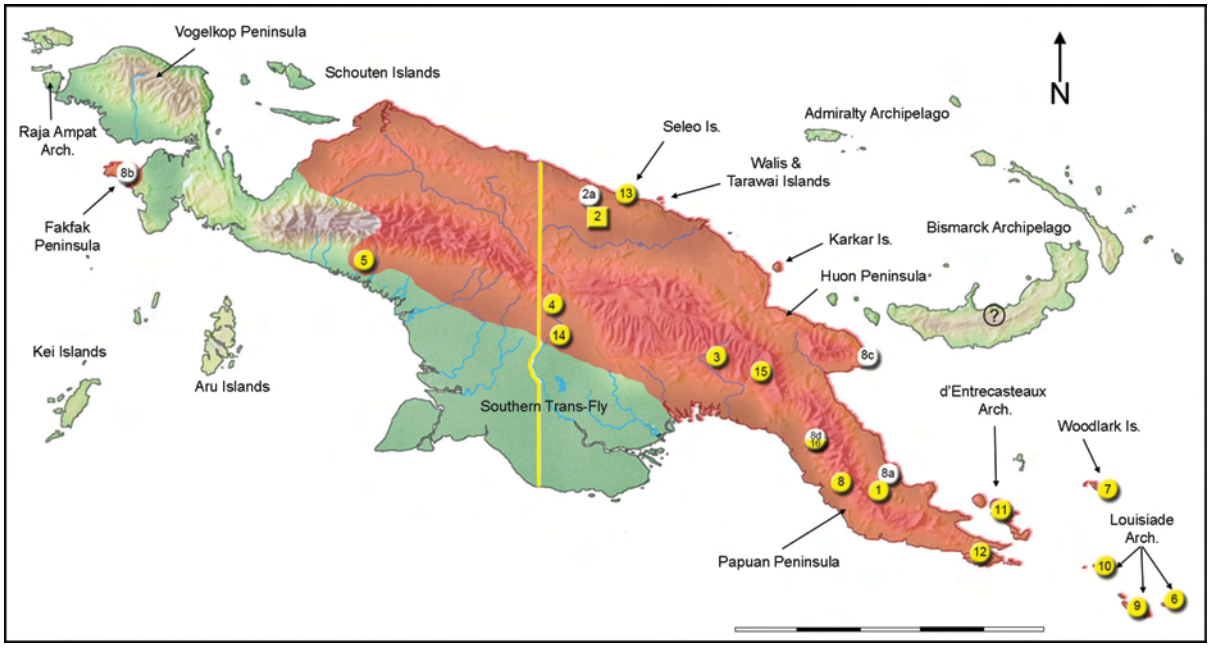

Figure 1. Map of New Guinea and surrounding islands, showing the mainland and offshore distribution of the genus *Toxicocalamus*, with the localities of type specimens indicated. The listed localities include those for types of currently recognized species (yellow circles), taxa in synonymy (white circles), and species without precise type locality data (yellow square). The portion of the map shaded in red indicates the known distribution of *Toxicocalamus*. The numbers inside the symbols correspond to the following listing, with synonyms identified by a lower case letter following the number of the valid species. Valid taxa are listed in alphabetical order following the new species. (1) Jarefa Camp, Itokama, Oro Province, PNG; holotype of *Toxicocalamus pumehanae* sp. nov. (BPBM 36185). (2) "German New Guinea," without precise locality data; holotype of *T. buergersi* (ZMB 25232); (2a) Torricelli Mountains, Sandaun Province, PNG; holotype of *Ultrocalamus latisquamatus*, synonym of *T. buergersi* (MTKD 2360, lost). (3) Haia, Crater Mountain Wildlife Management Area, Simbu Province, PNG; holotype of *T. cratermontanus* (USNM 562941); (4) Wangbin, Star Mountains, Western Province, PNG; holotype of *T. ernstmayri* (MCZ R-145946). (5) Launch Camp, Setekwa River, Papua Province, Indonesia; holotype of *T. grandis* (BMNH 1946.1.18.34). (6) Mount Rossel,

Rossel Island, Louisiade Archipelago, Milne Bay Province, PNG; holotype of *T. holopelturus* (AMNH R-76660). (7) Woodlark Island, Milne Bay Province, PNG; paralectotype and lectotype of *T. longissimus* (BMNH 1946.1.18.93). (8) Haveri, Bartholomew Range, Central Province, PNG; holotype of *T. loriae* (MSNG 29141). (8a) Mount Lamington, Oro Province, PNG; holotype and paratypes of *Apisthocalamus lamingtoni*, synonym of *T. loriae* (AM R-9351–52, 61027). (8b) Fakfak, Onin Peninsula, West Papua Province, Indonesia, syntypes of *A. loennbergii* (BMNH 1946.1.18.24–26, MCZ R-76634). (8c) Sattelberg, Huon Peninsula, Morobe Province, PNG; syntypes of *Pseudapistocalamus nymani*, synonym of *T. loriae* (BMNH 1946.1.17.57, MCZ R-76627–28, USPZ 2387). (8d) Dinawa, Central Province, PNG; holotype of *A. pratti,* synonym of *T. loriae* (BMNH 1946.1.14.53). (9) Mount Rio, Sudest Island, Louisiade Archipelago, Milne Bay Province, PNG; holotype of *T. mintoni* (BPBM 20822). (10) Mount Sisa, Misima Island, Louisiade Archipelago, Milne Bay Province, PNG; holotype of *T. misimae* (AMNH R-76684). (11) Oya Waka and Basima, Fergusson Island, d'Entrecasteaux Archipelago, Milne Bay Province, PNG; holotype and paratype of *T. nigrescens* respectively (BPBM 16545, 16544). (12) Cloudy Mountains, Milne Bay Province, PNG; holotype of *T. pachysomus* (BPBM 15771. (13) Seleo Island, Sandaun Province, PNG; paratype and holotype of *T. preussi preussi* (ZMB 23848). (14) Palmer Junction, Upper Fly River, Western Province, PNG; holotype of *T. preussi angusticinctus* (AMNH R-57511–12). (15) Purosa, Eastern Highlands Province, PNG; holotype of *T. spilolepidotus* (AMNH R-85745). (16) Same locality as 7d; holotype of *T. stanleyanus* (BMNH 1904.3.17.13). The type locality of *Vanapina lineata* (Vanapa River, Central Province, PNG), which some have considered a synonym of *T. longissimus*, is not illustrated due to loss of the specimen and lingering doubt over its correct placement into *Toxicocalamus*. The circled question mark in New Britain indicates Uasilau, the reported collection locality for an extant specimen of *Toxicocalamus*. Scale = 1000 km. N = North.

Figure 2. Holotype of *Toxicocalamus pumehanae* sp. nov. (BPBM 36185) in life, illustrating yellow pigment on supralabials, anterior head scutes, and conical tail cap. Photo by Allen Allison.

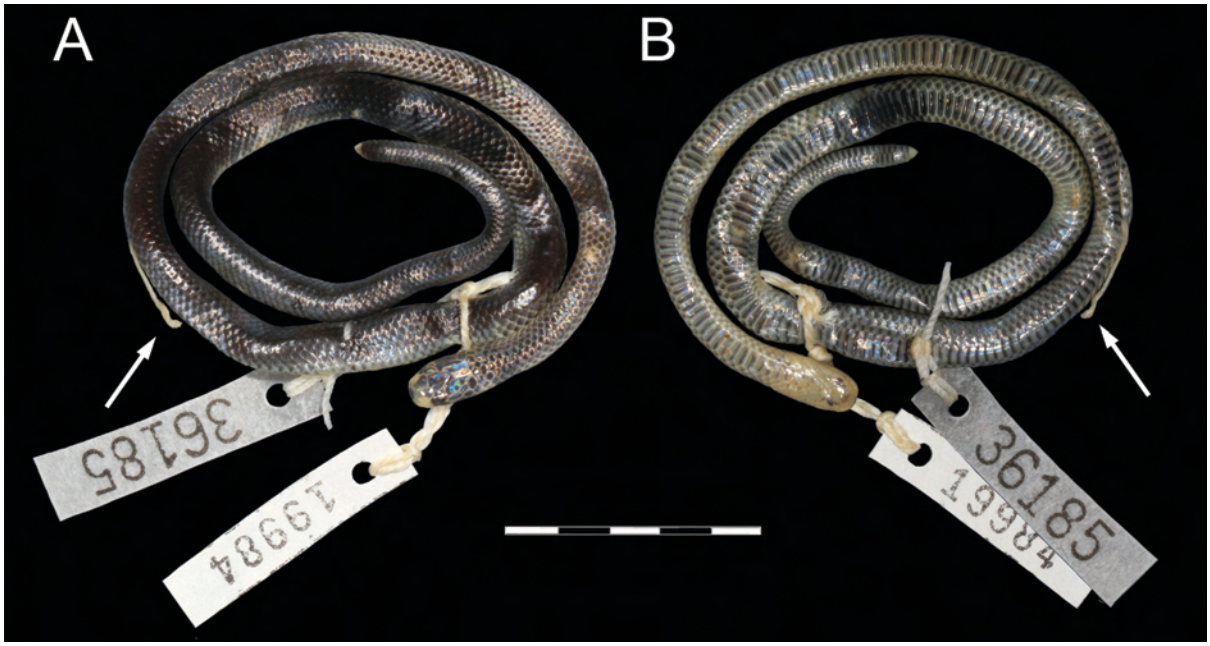

Figure 3. Holotype of *Toxicocalamus pumehanae* sp. nov. (BPBM 36185) in (A) dorsal and (B) ventral views. Scale = 5 cm.

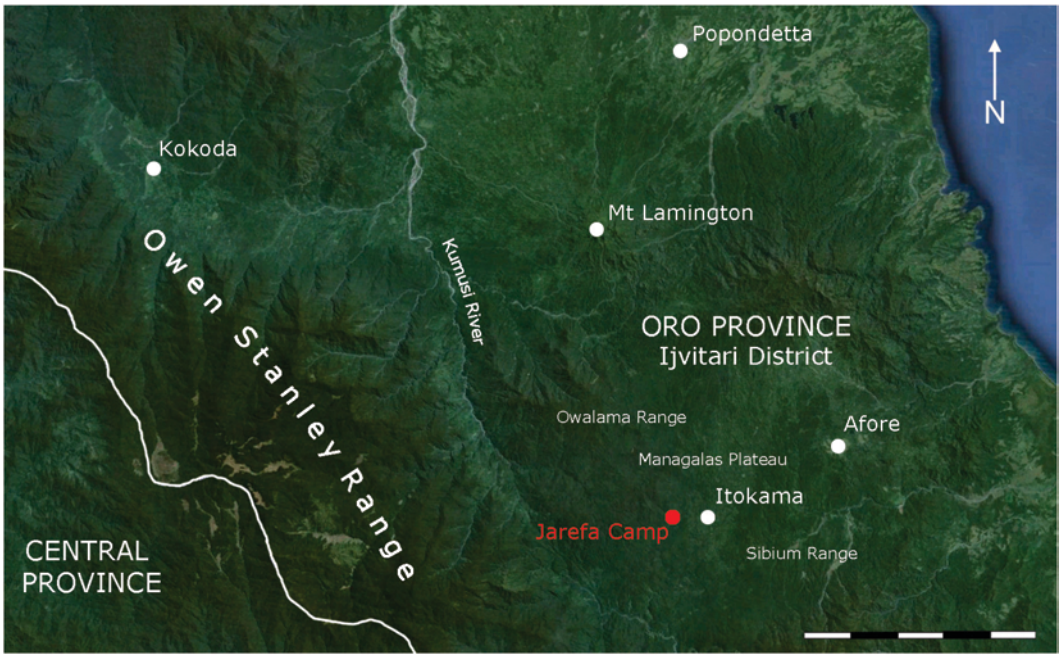

Figure 4. Satellite map of the region around Jarefa Camp, indicated by a red dot, the type locality for *Toxicocalamus pumehanae* sp. nov., on the eastern versant of the Owen Stanley Range, southern Oro Province, Papua New Guinea. Scale = 25 km. N = North.

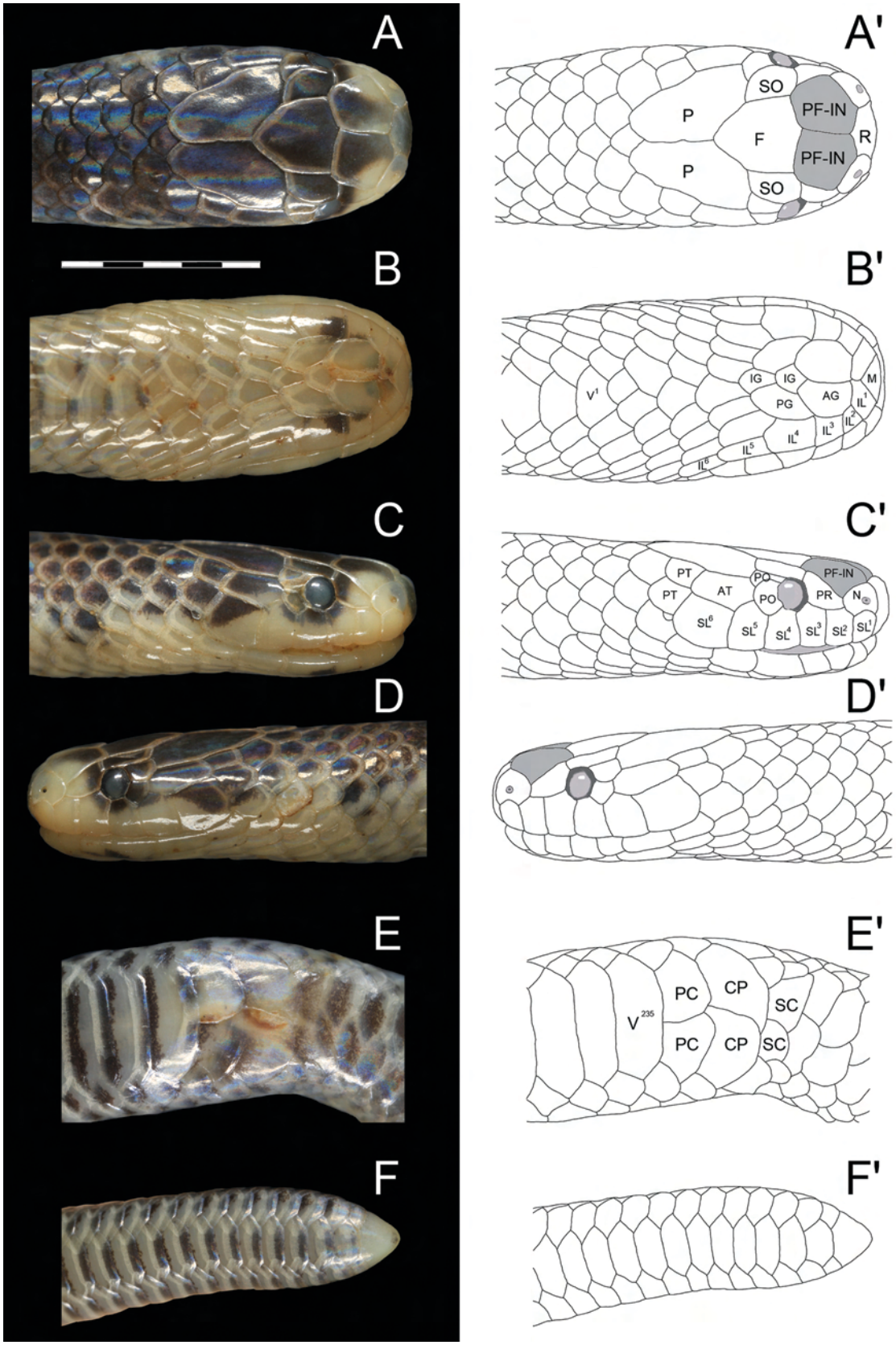

Figure 5. Detailed views of head and tail of *Toxicocalamus pumehanae* sp. nov. (BPBM 36185), presented for clarity as both photographic and line-drawn illustrations. (A, A′) Dorsal

1131 view of the head showing, rostal (R), fused prefrontal-internasals (PF-IN shaded), supraoculars
1132 (SO), frontal (F), and parietals (P). (B, B′) Ventral view, showing the scale arrangement of six
1133 infralabials (IL^1–IL^6), paired anterior genials (AG) and posterior genials (PG), intergenials (IG),
1134 the mental (M), and the first ventral scute (V^1). (C, C′) Right lateral view, showing undivided
1135 nasal (N), fused prefrontal-internasal (PF-IN shaded), a separate, single preocular (PR), paired
1136 postoculars (PO), a single anterior temporal (AT), and paired posterior temporals (PT). Six
1137 supralabials (SL^1–SL^6) are present, with SL^3 and SL^4 in contact with the orbit. (D, D′) Left
1138 lateral view, identical to left lateral view. (E, E′) Ventral view of the cloacal region showing
1139 the last ventral (V^{235}), paired precloacals (PC), paired cloacals (CP), and first subcaudals (SC).
1140 (F, F′) Lateral view of the laterally compressed tail, showing the conical terminal scale. The
1141 scale is 5.0 mm for the head views (A–D).
1142

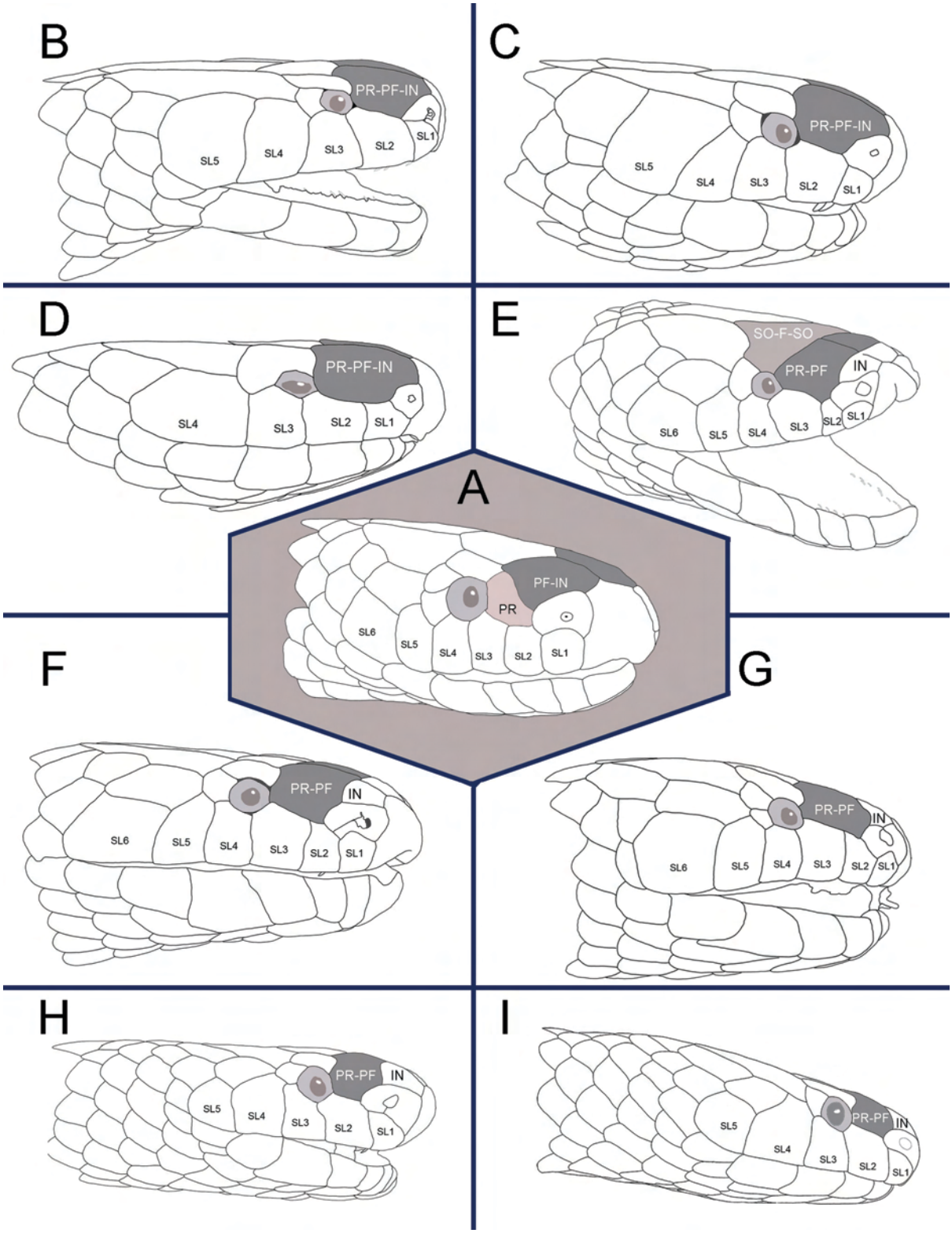

Figure 6. Fusion of dorsal head scutes and supralabial scale counts in various species of *Toxicocalamus*. Abbreviations include preocular (PR), prefrontal (PF), internasal (IN), supraocular (SO), frontal (F), and supralabial (SL). (A) BPBM 36185, holotype of *Toxicocalamus pumehanae* sp. nov., with separate PR and fused PF + IN. (B) AMNH 75001,

T. buergersi. The holotype of *T. buergersi* (ZMB 25232) is too desiccated to allow an accurate head drawing. (C) ZMB 23948, holotype of *T. preussi preussi*. (D) AMNH 57512, holotype of *T. p. angusticinctus*, with fused PR + PF + IN. (E) BPBM 20822, the holotype of *T. mintoni*, with separate IN, fused PR + PF, and fused SO + F + SO. (F) BMNH 1946.1.18.42, holotype of *T. longissimus*. (G) AMNH 76684, holotype of *T. misimae*. (H) BMNH 1946.1.17.55, holotype of *T. stanleyanus*. (I) USNM 562941, holotype of *T. cratermontanus*, with fused PR + PF. All other *Toxicocalamus* species exhibit the typical 'colubrid-elapid nine-scute arrangement,' in which all of these scutes are separated. Figures are not to scale.

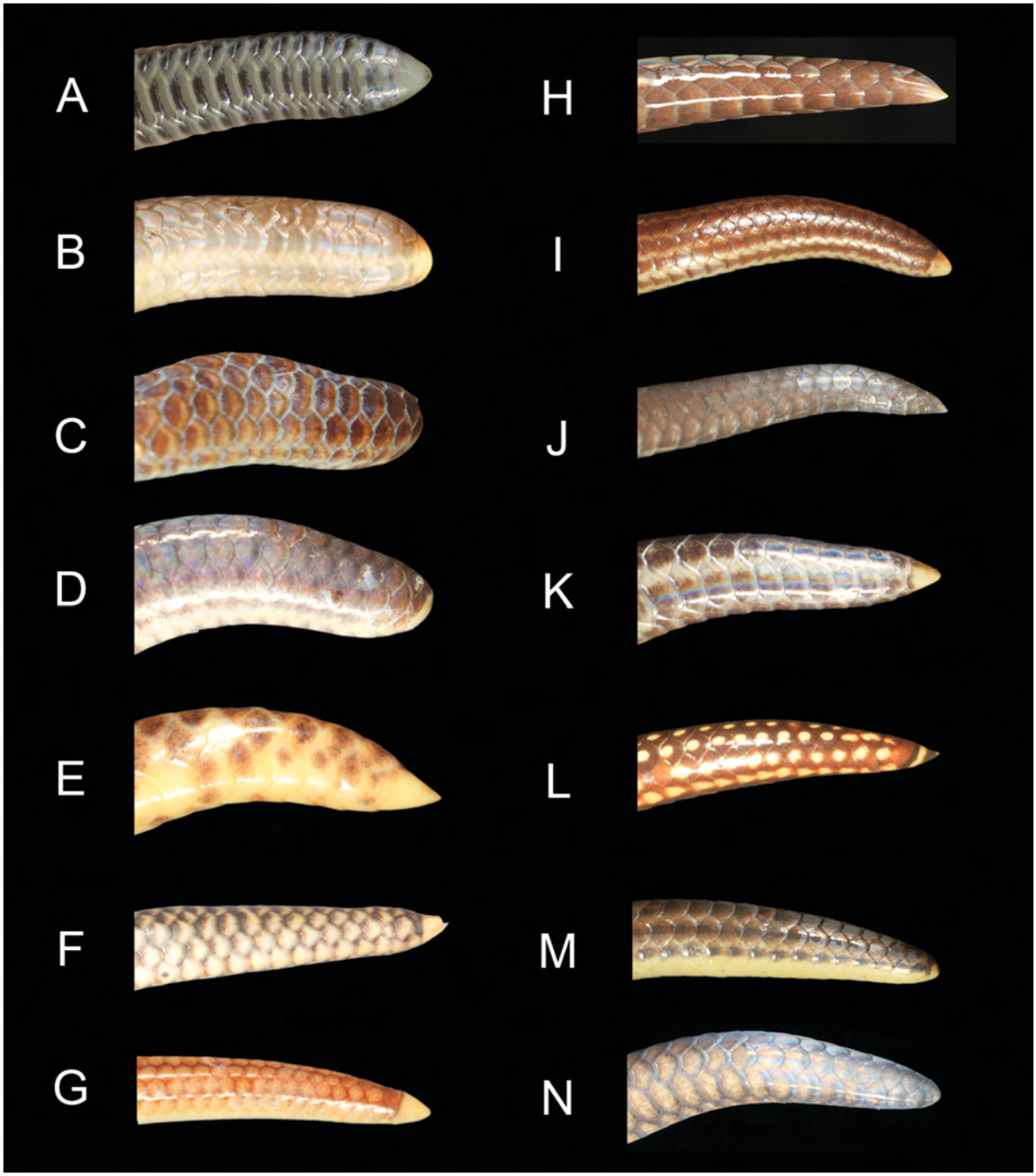

Figure 7. Tail tip shape and termination in various species of *Toxicocalamus*. (A) BPBM 36185, holotype of *T. pumehanae* sp. nov. (B) AMNH R-75236, *T. buergersi*. (C) ZMB 23948, holotype of *T. preussi preussi*. (D) AMNH R-75512, holotype of *T. p. angusticinctus*. (E) BMNH 1946.1.18.34, holotype of *T. grandis*. (F) MCZ R-145946, holotype *T. ernstmayri*. (G) UPNG 365, *T. loriae*. (H) BPBM 16545, holotype of *T. nigrescens*. (I) BMNH 1946.1.18.93, lectotype of *T. longissimus*. (J) BPBM 20829, *T. holopelturus*. (K) AMNH R-76684, holotype

of *T. misimae*. (L) PNGM 22132, *T. spilolepidotus*. (M) BMNH 1908.10.14.10, *T. stanleyanus*. (N) USNM 562941, holotype of *T. cratermontanus*. Figures are not to scale. Note: *Toxicocalamus mintoni* and *T. pachysomus* are known only from single specimens with truncated tails and are not included in this figure.

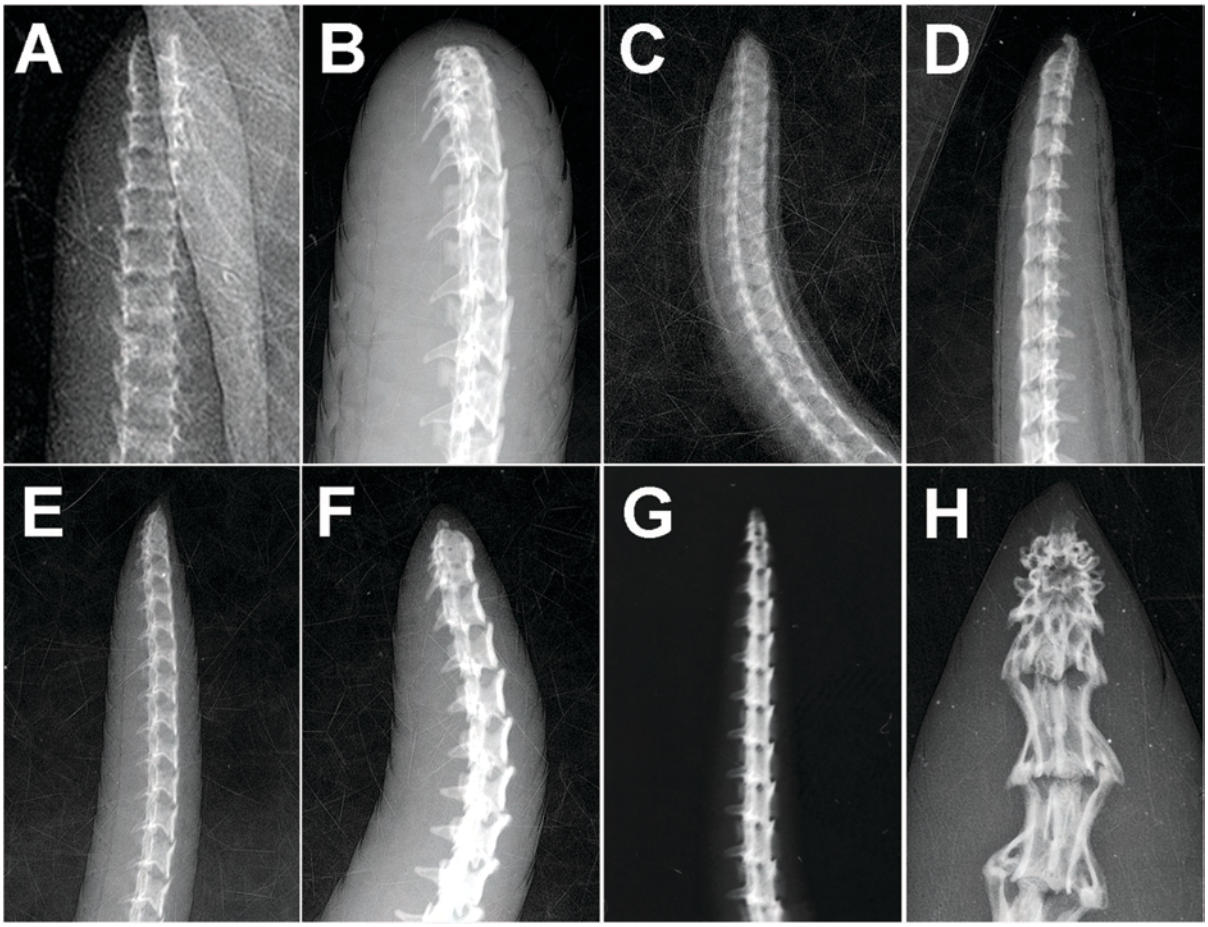

Figure 8. X-ray images of the tail tips of selected species of *Toxicocalamus*. (A) *T. pumehanae* sp. nov. (holotype; BPBM 36185). (B) *T. buergersi* (AM 129231). (C) *T. loriae* (paratype of *Apisthocalamus lamingtoni*; AM 9352). (D) *T. longissimus* (AM 124858). (E) *T. loriae* (BPBM 38855). (F) *T. misimae* (AM 125026). (G) *T. grandis* (holotype; BMNH 1946.1.18.34). (H) *T. ernstmayri* (holotype; MCZ R-145946).

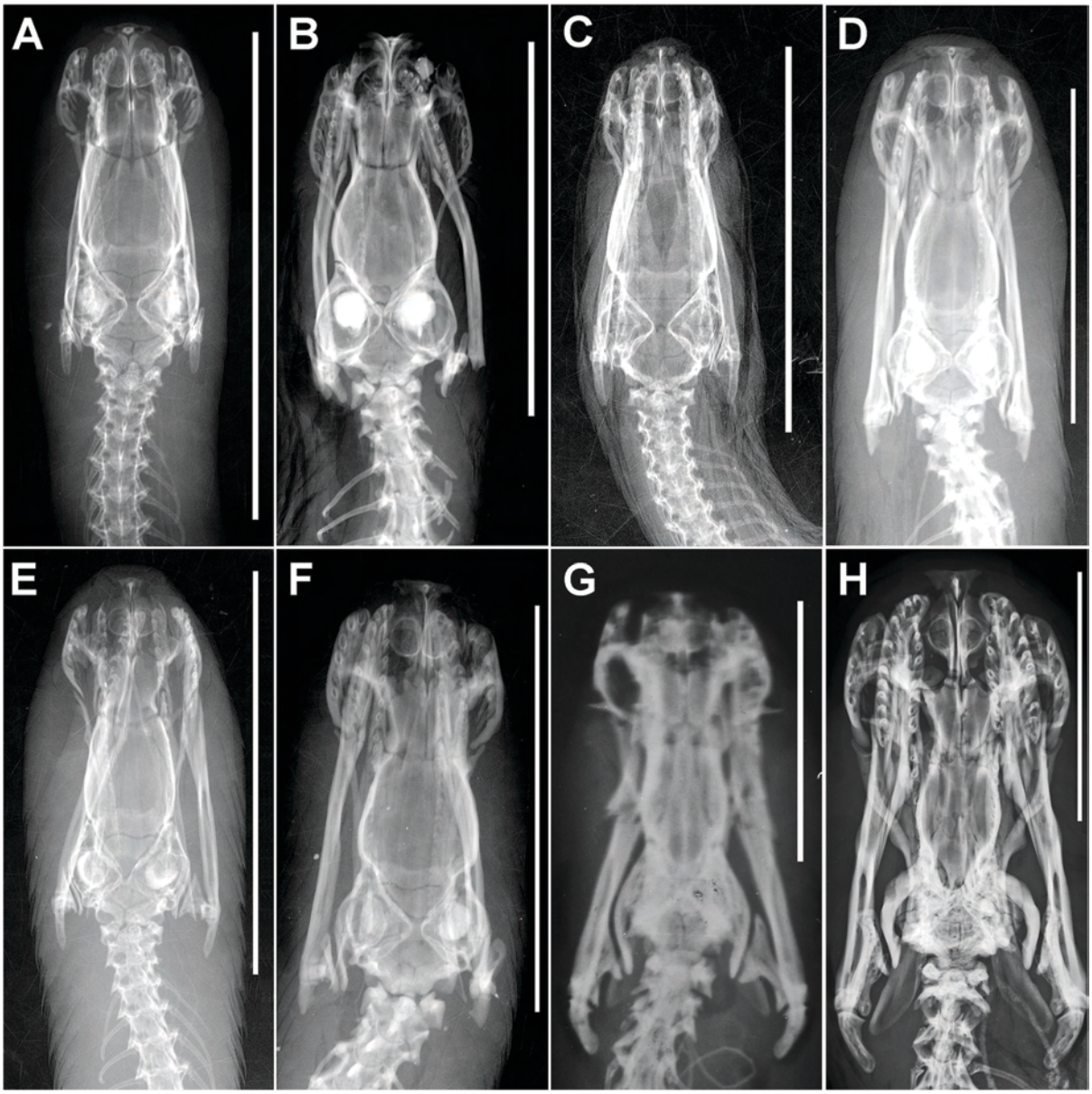

Figure 9. X-ray images of the skulls of selected species of *Toxicocalamus*. (A) *T. pumehanae* sp. nov. (holotype; BPBM 36185). (B) *T. buergersi* (AM 129231). (C) *T. loriae* (paratype of *Apisthocalamus lamingtoni*; AM 9352). (D) *T. longissimus* (AM 124858). (E) *T. loriae* (BPBM 38855). (F) *T. misimae* (AM 125026). (G) *T. grandis* (holotype; BMNH 1946.1.18.34). (H) *T. ernstmayri* (holotype; MCZ R-145946). Scales = 10 mm.

Supplementary material figure _____

Supplementary Data

Appendix 1. Comparative Material (*n* = 489)

Toxicocalamus buergersi (*n* = 6): PAPUA NEW GUINEA, EAST SEPIK PROVINCE: Wewak (elev. 200 m; 03º40’ S, 143º05’ E), AMNH R-75001, 75236; Maprik (elev. 195 m; 03°39' S, 143°02' E), AM R.120360, 129231. “Deutsch Neuguinea” [German New Guinea]: no further locality, ZMB 25232 (holotype). SANDAUN PROVINCE: Kumnatei (elev. 634 m; 03º27’ S, 142º05’ E) IRSNB 18736.

Toxicocalamus cratermontanus (*n* = 1): PAPUA NEW GUINEA, SIMBU PROVINCE: Haia, Crater Mountain Wildlife Management Area (elev. 920 m; 06º43’ S, 145º05’ E), USNM 562941.

Toxicocalamus ernstmayri (*n* = 1): PAPUA NEW GUINEA, WESTERN PROVINCE: Wangbin (elev. 1468 m; 5°14’ S, 141°16' E), MCZ R-145946 (holotype).

Toxicocalamus grandis (*n* = 1): INDONESIA, Papua Province: “Launch camp,” Setakwa River (elev. 25 m; 04º45’ S, 137º20’ E), BMNH 1946.1.16.34 (holotype).

Toxicocalamus holopelturus (*n* = 17): PAPUA NEW GUINEA, MILNE BAY PROVINCE: Rossel Is., Louisiade Archipelago, Mt. Rossel (elev. 205–700 m; 11º20’ S, 154º13’ E), AMNH R-76660 (holotype), BPBM 20823–33, PNGM 25194; Cheme (elev. 55 m; 11º19’ S, 154º14’ E), BPBM 20835–36; Mount Yuvu (elev. 450 m; 11º22’ S, 154º06’ E), MCZ R-156548; Gobubob (elev. 336 m; 11º21’ S, 154º09’ E), PNGM 25193.

Toxicocalamus longissimus (*n* = 17): PAPUA NEW GUINEA, MILNE BAY PROVINCE: Woodlark Island without precise locality data, (elev. n/a; 09º13’ S, 152º56’ E), BMNH 1946.1.18.92–93 (lectotype, paralectotype); Guasopa (elev. 12 m; 09º13’ S, 152º56’ E), AM R.124858, 124904, BPBM 17885–87; Kulumandau (elev. 53 m; 09º05’ S, 152º43’ E), AMNH R-76619, 76629–30, BPBM 42185; Suloga Harbour (elev. 80 m; 09º12’ S, 152º44’ E), BPBM 17888; Waimunon Bay (elev. 72 m; 09º04’ S, 152º50’ E), BPBM 39702; Dikoias (elev. 73 m; 09º02’ S, 152º45’ E), BPBM 42183–84; Fergusson Island (probably in error, *fide* O’Shea & Kaiser, *in prep*.), no further locality data, BMNH 1904.11.1.60. No locality data, AM R.46845.

Toxicocalamus loriae sensu lato (*n* = 312): PAPUA NEW GUINEA, CENTRAL PROVINCE: Haveri, Owen Stanley Range (elev. 700 m; 09º25’ S, 147º35’ E), MSNG 29141 (holotype of *Apistocalamus loriae*); Dinawa, Owen Stanley Range (elev. 1220 m; 08º35’ S, 145º55’ E), BMNH 1946.1.14.53 (holotype of *Apistocalamus pratti*); Mafulu, Owen Stanley Range (elev. 1270 m; 08º30’ S, 147º04’ E), AMNH R-59067, BMNH 1935.5.10.174; Fane to Bellavista road, Owen Stanley Range (elev. 1065 m; 08º32’ S, 147º05’ E), PNGM 23158; Tapini, Owen Stanley Range (elev. 950 m; 08º21’ S, 146º59’ E), USNM 195619; Owers Corner, Owen Stanley Range (elev. 620 m; 09º21’ S, 147º29’ E), MCZ R-150803; Siruohu and Mabiri stream, Mount Obree (elev. 1550 m; 09º26’ S, 140º00’ E), BPBM 19503–04; Laronu (elev. 900 m; 09º26’ S, 147º59’ E), BPBM 19502, 19505–06. MILNE BAY PROVINCE: Bunisi, Mount Simpson (elev. 1490 m; 10º01’ S, 149º36’ E), BPBM 17989, 18164, 18166; Siyomu, Mount Simpson (elev. 1300 m; 10º01’ S, 149º35’ E), BPBM 17987–88, 18165, 30638; Agaun, Mount Dayman (elev. 1014 m; 09º55’ S, 149º20’ E), PNGM 24649A–B, UPNG 4840; Dumae Creek, West Agaun, Mount Dayman (elev. 1200 m; 09º53’ S, 149º19’ E), BPBM 10966–67; Bonenau (elev. 1340 m; 09º53’ S, 149º24’ E), UPNG 7105, 7107–08; Mai-iu River (elev. 428 m; 09º41’ S, 149º16’ E), UPNG 3526. ORO PROVINCE: Itokama (elev. 780 m; 09º12’ S, 148º16’ E),

BPBM 36169, 36171; Umwate, Itokama, (elev. 943 m; 09º16’ S, 148º16’ E), BPBM 43028–29, 43032; Akupe Camp, Itokama (elev. 723 m; 09º17’ S, 148º16’ E), BPBM 43027; Mount Trafalgar, Cape Nelson (elev. 187 m; 09º13’ S, 149º09’ E), BPBM 39813; Isurava, Kokoda Trail (elev. 1260 m; 08º59’ S, 147º44’ E), BPBM 44892; Eora Creek, Kokoda Trail (elev. 1800 m; 00º02’ S, 147º44’ E), BPBM 44893; Kokoda Trail, no further locality data, PNGM 22762; ‘Popondetta’ (elev. 106 m; 08º46’ S, 148º14’ E), AMNH R-111810, MCZ R-141009; Imanaturu, Mt. Lamington (08°54' S, 148°12' E), AM R.9351–52, 61027 (holotype and paratypes of *Apisthocalamus lamingtoni*), AM R.9851. MOROBE PROVINCE: Garaina (elev. 770 m; 07º53’ S, 147º08’ E), MCZ R-152432; Saurere, West Garaina (elev. 1440 m; 07º55’ S, 147º05’ E), PNGM 22767; Saiko (elev. 1870 m; 07º57’ S, 147º03’ E), BPBM 41381, 41390; Amu Creek (elev. 1660 m; 07º55’ S, 147º02’ E), BPBM 41391; Waria Valley (elev. 485 m; 07º48’ S, 147º24’ E), BPBM 38855; Wau and environs (elev. 1220–2000 m; 07º20’ S, 146º43’ E), BPBM 17173, 17417, 17451–52, 18217, 23669, 36038, CAS 198320–22, KU 129086, PNGM 24716; Kalolo Creek (elev. 965 m; 07º18’ S, 146º43’ E), AMNH R-1422887, BPBM 5440, 5442; Hewieni, Kariba River (elev. 1050 m; 07º25’ S, 146º25’ E), BPBM 17423; Aseki, Watut Valley (elev. 1640 m; 07º20’ S, 146º10’ E), BPBM 6497; Kwaplalim, West of Menyamya, Tauri River (elev. 1500 m; 07º11’ S, 145º58’ E), UCM 51552–53, NMW 37670; Zenag, Markham Valley (elev. 940 m; 06º57’ S, 146º37’ E), AMNH R-85744; Sattelberg, Huon Peninsula (elev. 800 m; 06º29’ S, 147º47’ E), BMNH 1946.1.17.57 MCZ R-76627–28, UPSZ 2387 (syntypes of *Pseudapistocalamus nymani*); Masba Creek, Huon Peninsula (elev. 760 m; 06º29’ S, 147º31’ E), AMNH R-95579–80; Mount Rawlinson, Huon Peninsula (elev. 1340 m; 06º31’ S, 147º16’ E), AMNH R-95581; Pindui and environs, Huon Peninsula (elev. 790 m; 06º17’ S, 147º18’ E), AMNH R-95578, 95582; Boana, Huon Peninsula (elev. 1020 m; 06º25’ S, 146º50’ E), CAS 113668; Tuwop, Sarawaget Range, Huon Peninsula (elev. 1350 m; 06º21’ S, 146º55’ E), BPBM 3397, 3399; Lialun, Huon Peninsula (elev. 116 m; 06º06’ S,

147º36’ E), ZMB 24343–44, 78770–71. MADANG PROVINCE: Maibang (elev. 436 m; 05º38’ S, 146º18’ E), IRSNB 7336678; Astrolabe Bay (elev. 116 m; 05º22’ S, 145º39’ E), NMW 27383.1–2; Wanang (elev. 120 m; 05º15’ S, 145º16’ E), BPBM 31257; Bundi (elev. 1150 m; 05º44’ S, 145º14’ E), AM R.124482, Kalne River, Bismarck Range (elev. 1200 m; 05º31’ S, 144º49’ E), UPNG 8695; Kaironk, Kaironk Valley Schrader Range (elev. 1850 m; 05º14’ S, 144º29’ E), UPNG 963–67, 3353, 5012; Fungoi, Kaironk Valley Schrader Range (elev. 1800 m; 05º14’ S, 144º29’ E), AM R.23068–69, 23071–72; Matatambu, Adelbert Range (elev. 1140 m; 04º36’ S, 145º54’ E), UPNG 8695; Miak, Karkar Island (elev. 39 m; 04º36’ S, 145º54’ E), AM R.25236, 25304, 25752; Mom, Karkar Island (elev. 61 m; 04º38’ S, 145º53’ E), AM R.25608. EASTERN HIGHLANDS PROVINCE: Wonenara, Yaiya Valley (elev. 1650 m; 06º48’ S, 145º53’ E), UPNG 1213–18; Agakamatasa (elev. 1720 m; 06º43’ S, 145º37’ E), MCZ R-121545; Lida Patrol Post (elev. 1800 m; 06º19’ S, 145º23’ E), CAS 139575; Nivi Unggai (elev. 2030 m; 06º13’ S, 145º18’ E), MCZ R-84142, 116791–92; Lufa, Mount Michael (elev. 1120 m; 06º20’ S, 145º15’ E), CAS 113666–67, MCZ R-121546. SIMBU PROVINCE: Noru, Tua River, Karimui Plateau (elev. 1110 m; 06º30’ S, 144º50’ E), AM R.115365; Karimui, Karimui Plateau (elev. 1770 m; 05º59’ S, 144º55’ E), CAS 118961-62; Igindi, Suai Mountains (elev. 1630 m; 06º11’ S, 144º58’ E), AMNH R-98134; Kebil, Wahgi Valley (elev. 1944 m; 06º10’ S, 145º01’ E), MCZ R-85050; Kundiawa, Wahgi Valley (elev. 1585 m; 06º01’ S, 144º58’ E), AMNH R-98495–98, 103902, CAS 99916, 100069, 113669–71, 115986–6013, 118946–56, 118956, 118960, 139584, 140034–44, MCZ R-83218, 84026, 84143–44, 111764–90, 115586, 116774–88, 123883–86, 140818–19, 145923, NMV 13421, PNGM 864, 882, 24585–86, SAMA R9526, USNM 166280; Mintima, Wahgi Valley (elev. 1830 m; 05º58’ S, 144º55’ E), CAS 118957–59, MCZ R-116789–90; Poral Ras, Wahgi Valley (elev. 1770 m; 05º59’ S, 144º55’ E), CAS 103374–75, 113663, MCZ R-121547–48; Kondiu, Wahgi Valley (elev. 1600 m; 05º58’ S, 144º52’ E), AMNH R-75336–57; Kup, Wahgi Valley (elev. 1500 m; 05º57’ S,

144º48’ E), AMNH R-72780–81; Wahgi River, without precise locality data, CAS 113665–64. Jiwaka Province: Minj, Wahgi Valley (elev. 1560 m; 05º52’ S, 144º40’ E), MCZ R-141849; Banz, Wahgi Valley (elev. 1650 m; 05º47’ S, 144º37’ E), AMNH R-85743, 88060, Kimil, Wahgi Valley (elev. 1700 m; 05º43’ S, 144º32’ E), AM R.14783, 14785–88; Kol, Jimi Valley (elev. 1500 m; 05º42’ S, 144º50’ E), CAS 140042. WESTERN HIGHLANDS PROVINCE: Korn, Mt Hagen (elev. 1705 m; 05º51’ S, 144º18’ E), AM R.14771, 14473; Dobel, Mount Hagen (elev. 1705 m; 05º51’ S, 144º14’ E), PNGM 22160, UPNG 3992, Baiyer River (elev. 1170 m; 05º31’ S, 144º10’ E), AM R.16575, 16581. SOUTHERN HIGHLANDS PROVINCE: Mendi (elev. 1750 m; 06º08’ S, 143º39’ E), CAS 113664, MCZ R-121543–44; Halalinja, Waga River (elev. 2140 m; 06º09’ S, 143º22’ E), BMNH 1976.92; Nipa (elev. 2070 m; 06º06’ S, 143º15’ E), UPNG 5811; Moro Camp, Lake Kutubu (elev. 840 m; 06º21’ S, 143º13’ E), SAMA 69950; Bobole (elev. 1145 m; 06º12’ S, 142º46’ E), AM R.122803, 122806. SANDAUN PROVINCE: Busilmin, Star Mountains (elev. 1880 m; 04º55’ S, 141º12’ E), SAMA R.6275. “Neuguinea” [New Guinea], no further locality, NMW 27382.1–2. “Deutsch Neuguinea” [German New Guinea], no further locality, ZMB 23533, ZSM 244/1926. INDONESIA, WEST PAPUA PROVINCE: Fak Fak Peninsula (elev. 518 m; 02º57’ S, 132º35’ E), BMNH 1946.1.18.24–26, MCZ R-76634 (holotype and paratypes of *Apistocalamus loennbergii*). “New Guinea,” no further locality, MZB 361. No locality data, AM R.46844.

Toxicocalamus mintoni (*n* = 1): PAPUA NEW GUINEA, MILNE BAY PROVINCE: Mount Riu, Sudest Island, Louisiade Archipelago (elev. 410 m; 11º29’ S, 153º25’ E), BPBM 20822 (holotype).

Toxicocalamus misimae (*n* = 6): PAPUA NEW GUINEA, CENTRAL PROVINCE: Mekeo Region (09°00' S, 146°50' E), (probably in error, *fide* O’Shea & Kaiser, *in prep*.), AM R.7614. MILNE

BAY PROVINCE: Umuna Mine, Misima Island, Louisiade Archipelago, (elev. 130 m; 10º40’ S, 152º48’ E), AM R.125026; Mararoa, Mount Sisa, Misima Island, Louisiade Archipelago, (elev. 350 m; 10º39’ S, 152º48’ E), AMNH R-76684 (holotype); Misima Mine, Misima Island, Louisiade Archipelago, (elev. 180 m; 10º39’ S, 152º47’ E), SAMA 69921; Bulai Plantation, Misima Islands, Louisiade Archipelago, (elev. 180 m; 10º39’ S, 152º45’ E), SAMA 69924; Bagilina, Mt. Oia-Tau, Misima Island, Louisiade Archipelago, (elev. 128 m; 10º39’ S, 152º48’ E), BPBM 17231.

Toxicocalamus nigrescens (*n* = 2): PAPUA NEW GUINEA, MILNE BAY PROVINCE: Basima, Fergusson Island, d’Entrecasteaux Archipelago (elev. 10 m; 09º28’ S, 150º50’ E), BPBM 16544; Oya Waka, Fergusson Island, d’Entrecasteaux Archipelago (elev. 990 m; 09º27’ S, 150º33’ E), BPBM 16545.

Toxicocalamus pachysomus (*n* = 1): PAPUA NEW GUINEA, MILNE BAY PROVINCE: Gadowalai, Cloudy Mountains (elev. 715 m; 10º29’ S, 150º14’ E), BPBM 15771 (holotype).

Toxicocalamus preussi (*n* = 59): PAPUA NEW GUINEA, SIMBU PROVINCE: Crater Mountain (elev. 2325 m; 06º35’ S, 145º05’ E), BPBM 17449; Haia (elev. 908 m; 06º43’ S, 145º05’ E), USNM 562943–44. GULF PROVINCE: Weiana, Pio River (elev. 444 m; 06º45’ S, 144º52’ E), CAS 118945; Wabo (elev. 400 m; 06º54’ S, 145º03’ E), USNM 562942; Koni (= Pawaia No. 2), Purari River (elev. 76 m; 07º15’ S, 145º20’ E), MCZ R-102176; Middletown, Kikori River (elev. 63 m; 07º16’ S, 144º09’ E), MCZ R-59090; Kopi Camp, Kikori River (elev. 22 m; 07º19’ S, 144º11’ E), SAMA 69947–48; NW of Kikori, Kikori River (elev. 37 m; 07º10’ S, 144º05’ E), MCZ R-150804. SOUTHERN HIGHLANDS PROVINCE: Waro, Hegigio River (elev. 470 m; 06º32’ S, 143º11’ E), AM R.122811–12; Fogamaiyu, Hegigio River (elev. 230 m; 06º31’ S,

143º05’ E), AM R.122805; Didessa, Mt. Bosavi (elev. 1885 m; 06º34’ S, 142º50’ E), ZSM 19/1966; Namosado, Mt. Sisa (elev. 870 m; 06º15’ S, 142º47’ E), AM R.122808. WESTERN PROVINCE: south of Palmer Junction, Strickland River (elev. 65 m; 05º54’ S, 141º32’ E), AMNH R-57511–12 (holotype and paratype of *Ultrocalamus preussi angusticinctus*); Matkomrae, Ok Tedi (elev. 82 m; 05º49’ S, 141º09’ E), MCZ R-121551, 141008; Ningerum, Ok Tedi (elev. 86 m; 05º41’ S, 141º08’ E), MCZ R-140989, 141007, PNGM 22159, USNM 217500; Tabubil, Ok Tedi (elev. 457 m; 05º15’ S, 141º12’ E), AM R.127468, UPNG 5665; Olsobip, Fly River (elev. 612 m; 05º23’ S, 141º31’ E), PNGM 24584, UPNG 1613, Kataw (= Binaturi River), Southern Trans-Fly (probably in error, *fide* O’Shea & Kaiser, *in prep*.) (elev. 0 m; 09º08’ S, 142º57’ E), MSNG 54100. EAST SEPIK PROVINCE: Wewak (elev. 53 m; 03º35’ S, 143º38’ E), AM R.95600. SANDAUN PROVINCE: Berlinhafen, Seleo Island (elev. 13 m; 03º08’ S, 142º29’ E), ZMB 23948 (holotype of *Ultrocalamus preussi*); Mount Sapau, Torricelli Range (elev. 1300 m; 03º22’ S, 142º31’ E), BPBM 23456; Parkop, Mt Sapau, Torricelli Range Range (elev. 560 m; 03º23’ S, 142º31’ E), AM R.115505; Wilbeite (elev. 866 m; 03º25’ S, 142º07’ E), AM R.136279; Mt. Boobiari (elev. 400 m; 04º35’ S, 141º10’ E), AM R.115507; Enemb River (elev. 550 m; 03º16’ S, 141º11’ E), AM R.135501; Njao, Tjano River (elev. 450 m; 02º48’ S, 141º00’ E), ZMA.RENA 17733. WEST NEW BRITAIN PROVINCE: Uasilau (questionable) (elev. 117 m; 05º34’ S, 150º52’ E), IRSNB 18737. INDONESIA, PAPUA PROVINCE: Arso, Tami River (elev. 53 m; 02º56’ S, 140º47’ E), ZMA.RENA 17734B; Hollandia [= Jayapura], (elev. 100 m; 02º532’ S, 140º42’ E), FMNH 43030, ZMA.RENA 17735; Upper Sermowai River (elev. 95 m; 02º29’ S, 139º50’ E), UIMNH 19199, ZMA.RENA 17736A–C; Etik, Biri River (elev. 140 m; 02º17’ S, 139º08’ E), MZB 5090, ZMA.RENA 17734A; SW of Bernard Camp, Idenberg River (elev. 800–850 m; 03º30’ S, 139º09’ E), AMNH R-62469–72; Prauwenbivak, Idenberg River (elev. 40 m; 02º25’ S, 139º10’ E), MZB 354, 5089, ZMA.RENA 17731; Albatrosbivak, Mamberamo River (elev. 40 m; 02º09’ S,

137º52’ E), MZB 356, 5054–56; Pionierbivak, Mamberamo River (elev. 10 m; 02º04’ S, 137º50’ E), ZMA.RENA 17732; Mamberamo River (elev. 20 m; 01º55’ S, 137º50’ E), MZB 353. No locality data, AM R.46847.

Toxicocalamus pumehanae (*n* = 1) PAPUA NEW GUINEA, ORO PROVINCE: Jarefa Camp, Itokama (elev. 820 m; 09°12'19" S, 148°14'15" E) BPBM 36185.

Toxicocalamus spilolepidotus (*n* = 2): PAPUA NEW GUINEA, Eastern Highlands Province: Purosa, Okapa (elev. 1740 m; 06º40’ S, 145º33’ E), AMNH R-85745 (holotype); Yaiya Valley, Kratke Mountains (elev. 1500 m; 07º00’ S, 145º49’ E), PNGM 21332.

Toxicocalamus stanleyanus (*n* = 42): PAPUA NEW GUINEA, CENTRAL PROVINCE: Dinawa, Owen Stanley Range (elev. 840 m; 08º35’ S, 146º55’ E), BMNH 1946.1.7.55 (holotype), 1904.3.17.13; Madew, St. Joseph River, Owen Stanley Range (elev. 1200 m; 08º36’ S, 146º55’ E), BMNH 1908.10.14.10–12; Mafulu, Owen Stanley Range (elev. 1270 m; 08º30’ S, 147º04’ E), AMNH R-59063, BMNH 1935.5.10.171–173; Maeaera Plantation (elev. 7 m; 08º40’ S, 146º31’ E), ZSM 52/2000. GULF PROVINCE: Teduku, Eloa River (elev. 178 m; 07º43’ S, 146º29’ E), USNM 562945; Middletown, Kikori River (elev. 63 m; 07º16’ S, 144º09’ E, MCZ R-59059–60, USNM 217499. Unknown locality, UPNG 8737A–B. SIMBU PROVINCE: Camp II, Pio River (elev. 300 m; 06º44’ S, 144º52’ E), MCZ R-121549; Soliabeda, Ining River (elev. 457 m; 06º41’ S, 144º52’ E), CAS 118943. SOUTHERN HIGHLANDS PROVINCE: Waro, Hegigio River (elev. 470 m; 06º32’ S, 143º11’ E), AM R.122809–10; Fogamaiyu, Hegigio River (elev. 230 m; 06º31’ S, 143º05’ E), AM R.122804; Didessa, Mt. Bosavi (elev. 1885 m; 06º34’ S, 142º50’ E), ZSM 49–52/2000, 71/2015; Namosado, Mt. Sisa (elev. 870 m; 06º15’ S, 142º47’ E), AM R.122807. WESTERN PROVINCE: Matkomrae, Ok Tedi (elev. 82 m; 05º49’ S, 141º09’

E), MCZ R-121550; Ningerum, Ok Tedi (elev. 86 m; 05º41’ S, 141º08’ E), MCZ R-140988; Derongo, Ok Taub (elev. 615 m; 05º26’ S, 141º08’ E), CAS 121220. MADANG PROVINCE: Road from Hinihon to Reinduk, Adelbert Range (elev. 1000 m; 04º40’ S, 145º22’ E), BPBM 5711. EAST SEPIK PROVINCE: Arin (elev. 560 m; 03º33’ S, 143º20’ E), UPNG 7171. SANDAUN PROVINCE: Mount Nibo, S of Aitape (elev. 208 m; 03º23’ S, 142º09’ E), AMNH R-100047; Parkop, Mount Sapau, Torricelli Range (elev. 526 m; 03º25’ S, 142º31’ E), BPBM 223455. INDONESIA, PAPUA PROVINCE: Ingembit, Ok Walimkan (elev. 117 m; 05º38’ S, 141º00’ E), MZB 1464; Canobivak, Eilanden River (elev. 37 m; 05º14’ S, 139º40’ E), ZMA.RENA 17682; Beaufort River Camp, Baliem Valley (elev. 64 m; 03º27’ S, 139º10’ E), RMNH.RENA 4988, 47753–54; Siewa (elev. 80 m; 03º03’ S, 136º22’ E), MZB 2784. WEST PAPUA PROVINCE: Fak Fak Regency, Bomberai Peninsula (elev. 380–520 m; 02º57’ S, 132º35’ E), ZMA.RENA 17683. No locality data, AM R.46846, 46848.

Toxicocalamus sp. (*n* = 19): PAPUA NEW GUINEA, MILNE BAY PROVINCE: Samarai Island (elev. n/a; 10º37’ S, 150º40’ E), AM R.5038. MOROBE PROVINCE: Garaina (elev. 770 m; 07º53’ S, 147º08’ E), AMNH R-95624, 101100–03, 103681, 104084–85, 107203–05; MCZ R-152428–31. MADANG PROVINCE: Fungoi, Kaironk Valley Schrader Range (elev. 1800 m; 05º14’ S, 144º29’ E), AM R.23073. INDONESIA, PAPUA PROVINCE: Angurruk, Jahûli River (elev. 1450 m; 04º12’ S, 139º26’ E), ZSM 54/2015, Dingerkon, Eipomek River (elev. 1800 m; 04º27’ S, 140º01’ E), ZSM 55/2015.

Appendix 2. Other Material Examined (*n* = 94)

Aspidomorphus muelleri (*n* = 3): PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12’ S, 148º16’ E), BPBM 36168, 36178; Umwate (elev. 943 m; 09°08'13"S, 148°23'13"E), BPBM 43027.

Aspidomorphus schlegelii (*n* = 87): PAPUA NEW GUINEA, SANDAUN PROVINCE: Aitape (elev. 15 m; 03º08’ S, 142º20’ E), AM R.8895; Parkop and environs, Mt. Sapau, Torricelli Range (elev. 420–600 m; 03º25’ S, 142º31’ E), BPBM 23433–34; Unknown locality AM R.11826, 11896, 133504, BPBM 35967. INDONESIA, PAPUA PROVINCE: Hollandia (= Jayapura) (elev. 20 m; 02º32’ S, 140º43’ E), RMNH.RENA 45546–47; Bivak Boswezen, Tami River (elev. 15 m; 02º41’ S, 140º51’ E), RMNH.RENA 45546; Lake Sentani (elev. 90 m; 02º36’ S, 140º37’ E), RMNH.RENA 6305A–B; Djamna Island (elev. 14 m; 02º00’ S, 139º15’ E), MCZ R-7080 (holotype of *Pseudelaps muelleri insulae*); Seroie, Yapen Island, Schouten Islands (elev. 30 m; 01º52’ S, 135º49’ E), RMNH.RENA 45558; Ansus, Yapen Island, Schouten Islands (elev. 18 m; 01º43’ S, 136º14’ E), NMW 27395/2; Yapen Island without precise locality data, Schouten Islands (elev. n/a; 01º46’ S, 136º13’ E), RMNH.RENA 6309, 45525, 45528; Biak Island, Schouten Islands (elev. 100 m; 01º10’ S, 136º04’ E), RMNH.RENA 45560; Numfoor Island, Schouten Islands (elev. 90 m; 01º01’ S, 134º53’ E), NMW 27390/4–5, 27392/3–4; Merauke (probably in error) (elev. 20 m; 08º27’ S, 140º25’ E), MNV D.7574. WEST PAPUA PROVINCE: Lobo, Triton Bay (elev. 57 m; 03º44’ S, 134º06’ E), RMNH.RENA 1403 (syntype of *Elaps muelleri*); Wasior, Wandammen Bay (elev. 130 m; 02º43’ S, 134º30’ E), NRM 17810; Tamarome (elev. 52 m; 02º49’ S, 133º38’ E), RMNH.RENA 5107; Babo, Bintuni Bay (elev. 27 m; 02º32’ S, 133º25’ E), RMNH.RENA 6742A–B; Fak Fak Regency, Bomberai Peninsula (elev. 380–520 m; 02º57’ S, 132º35’ E), MCZ R-7311, RMNH.RENA 6306A–B, NMW 23489 (holotype of *Pseudelaps muelleri concolor*); “Jack Jack” (= Fak Fak?) NMW 27390/4–5; 10 km NE Steenkool, Vogelkop (elev. 130 m; 02º03’ S, 134º05’ E), NRM 17801; Manokwari, Vogelkop (elev. 10 m; 00º52’ S, 133º25’ E), RMNH.RENA 45541–45, 45566–69; Pasir Poetih, Manokwari, Vogelkop (elev. 25 m; 00º52’ S, 134º05’ E), RMNH.RENA 45570–72; Mansinam Island (sealevel; 00º54’ S,

134º05’ E), NMW 27390/2–3; Ajamaroe, Vogelkop (elev. 335 m; 01º16’ S, 132º10’ E), RMNH.RENA 45562–63, 45577; Atinyu, Lake Danau, Vogelkop (elev. 235 m; 01º26’ S, 132º023’ E), NRM 17809, 17812; Kamboeaja, Vogelkop (elev. 326 m; 01º17’ S, 132º14’ E), RMNH.RENA 45573–74; Vogelkop without precise locality (elev. n/a; 01º15’ S, 132º50’ E), RMNH.RENA 45514–17, 45521–23, 45526–27, 45530–40, 45556–57; Salawati Island, Raja Ampat Islands (elev. n/a; 01º07’ S, 130º52’ E), MCZ R-38967, RMNH.RENA 6307A–B; Batanta Island, Raja Ampat Islands (elev. n/a; 00º050’ S, 130º39’ E), RMNH.RENA 6308; Waigeo Island, Raja Ampat Islands (elev. n/a; 00º11’ S, 130º39’ E), RMNH.RENA 5623; Misool Island, Raja Ampat Islands (elev. n/a; 01º53’ S, 130º05’ E), BMNH 1946.1.18.43 (holotype of *Aspidomorphus schlegelii*). West New Guinea without locality data, IRSNB 11701.

Micropechis ikaheka (*n* = 5): PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12’ S, 148º16’ E), BPBM 36146, 36148, 43083; Druze Guest House, Itokama (elev. 766 m; 09º12’ S, 148º15’ E), BPBM 43012; Jarefa Camp, Itokama (elev. 820 m; 09º12’ S, 148º14’ E), BPBM 36187.

Appendix 3. Non-elapid Snakes Recorded in the Vicinity of Itokama (*n* = 73)

Indotyphlops braminus (*n* = 8) PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12’ S, 148º16’ E), BPBM 36170, 36173–74, 36177, 36178, 36181, unregistered [AA 19828]); Druze Guest House, Itokama (elev. 766 m; 09º12’ S, 148º15’ E), BPBM 43021.

Ramphotyphlops sp. (*n* = 6) PAPUA NEW GUINEA, ORO PROVINCE: Jarefa Camp, Itokama (elev. 820 m; 09º12’ S, 148º14’ E), unregistered [AA 19781]).

Gerrhopilus inornatus (*n* = 1) PAPUA NEW GUINEA, ORO PROVINCE: Afore (elev. 673 m; 09°08'13"S, 148°23'13"E), MCZ R-140724.

Candoia aspera schmidti (*n* = 6) PAPUA NEW GUINEA, ORO PROVINCE: Umwate (elev. 943 m; 09°08' S, 148°23'E), BPBM 42996–97, 43000; Akupe Camp (elev. 723 m; 09°08' S, 148°23'E), BPBM 42995, 42998–99.

Candoia paulsoni macdowelli (*n* = 4) PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12' S, 148º16' E), BPBM 36175; Umwate (elev. 943 m; 09°08' S, 148°23'E), BPBM 43006–08.

Candoia sp. (*n* = 1) PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12' S, 148º16' E), unregistered [AA 19781].

Morelia viridis (*n* = 11) PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12' S, 148º16' E), BPBM 36143, 36149, 36182–83; Umwate (elev. 943 m; 09°08' S, 148°23'E), BPBM 43014–20.

Simalia amethistina (*n* = 1) PAPUA NEW GUINEA, ORO PROVINCE: Druze Guest House, Itokama (elev. 766 m; 09º12' S, 148º15' E), BPBM 43013.

Boiga irregularis (*n* = 5) PAPUA NEW GUINEA, ORO PROVINCE: Umwate (elev. 943 m; 09°08' S, 148°23' E), BPBM 43001–02, 43004; Jarefa Camp, Itokama (elev. 820 m; 09º12' S, 148º14' E), unregistered [AA 19983]; Kamua (elev. 722 m; 09°17' S, 148°17' E), BPBM 43003.

Dendrelaphis sp. (*n* = 5) PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12’ S, 148º16’ E), BPBM 36180; Jarefa Camp, Itokama (elev. 820 m; 09º12’ S, 148º14’ E), BPBM 36186, unregistered [AA 18389]); Druze Guest House, Itokama (elev. 766 m; 09º12’ S, 148º15’ E), BPBM 43011; Akupe Camp (elev. 723 m; 09°08’ S, 148°23’ E), BPBM 43010.

Stegonotus sp. (*n* = 12) PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12’ S, 148º16’ E), BPBM 36144–45, 36169, 36171, unregistered [AA 19701, 19657, 19884]); Jarefa Camp, Itokama (elev. 820 m; 09º12’ S, 148º14’ E), BPBM 36142, 36189; Umwate (elev. 943 m; 09°08’ S, 148°23’ E), BPBM 43030–31, 43033.

Tropidonophis multiscutallatus (*n* = 1) PAPUA NEW GUINEA, ORO PROVINCE: Afore (elev. 673 m; 09°08’ S, 148°23’ E), MCZ R-139414.

Tropidonophis sp. (*n* = 14) PAPUA NEW GUINEA, ORO PROVINCE: Itokama (elev. 780 m; 09º12’ S, 148º16’ E), BPBM 36167, 36172, unregistered [AA 19905, 19556]); Jarefa Camp, Itokama (elev. 820 m; 09º12’ S, 148º14’ E), BPBM 36176, 36184, 36188; Druze Guest House, Itokama (elev. 766 m; 09º12’ S, 148º15’ E), BPBM 42988–89; Akupe Camp (elev. 723 m; 09°08’ S, 148°23’ E), BPBM 42987, 42993; Umwate (elev. 943 m; 09°08’ S, 148°23’ E), BPBM 42986, 42992, 42994.

Figure 10. Habitat at the type locality for *Toxicocalamus pumehanae* sp. nov. near Jarefa Camp, Itokama, Oro Province, Papua New Guinea. Photo by Allen Allison.